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The Canadian Entomologist

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The Humidity Reactions of *Melanoplus bivittatus* (Say) (Orthoptera, Acrididae): Antennal Sensilla and Hygro-reception[1]

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Hygro-receptive sensilla have been found on the antennae of fruit flies (1), spider beetles (2), cockroaches (3), wireworms (5), ticks (6), mealworm beetles (8), flour beetles (11), and body lice (16). Two types of antennal sensilla, the basiconic and the coeloconic, have been identified as hygro-receptors of the grasshoppers, *Melanoplus differentialis* (Thos.) and *M. mexicanus mexicanus* (Sauss.) (12, 13). This paper describes the antennal sensilla of *Melanoplus bivittatus* (Say) and discusses their function.

Methods

The type and number of sensilla were determined by examining the mounted antennae, magnified 180x and 810x, of 14 individuals from each nymphal stadium and from each sex of adults. Mounts of whole antennae were prepared from material preserved in 70 per cent ethanol. The insects were boiled in a ten per cent solution of potassium hydroxide to soften and clear the cuticle, and then washed in running water to remove the alkali. With the aid of a binocular microscope the antennae were removed from the head, under water, with a pair of dissecting needles and delicate forceps. They were dehydrated with alcohol in the usual way and mounted in euparol on glass slides.

The internal structure of the sensilla was determined by examining histological sections of antennae, magnified 1800x. Nymphs of the first four instars were fixed *in toto* in Bouin's fixative but only the heads of fifth instar nymphs and of adults were so treated. The fixed and cleared antennae were embedded in 'Tissuemat' (Fisher Scientific Co. Ltd., Toronto, Ontario) at 52° to 54° C., and sectioned on a Spencer rotary microtome at six to 10 microns. Fixed and cleared antennae were also embedded in a n-butyl metacrylate (7), and sectioned at one to two microns. Sections were stained with eosin, Heidenhain's iron haematoxylin or haematoxylin-eosin and mounted in Canada balsam.

The location and distribution of hygro-receptors was determined by testing, in an olfactometer (9, 10), the humidity reactions of groups of adults that had undergone a series of antennal and palpal operations. Amputations were carried out under a binocular microscope using a pair of delicate iridectomy scissors and a micro-scalpel. Each test insect was subjected to only one amputation. The insects were given a choice between 0 and 90 per cent relative humidity in the olfactometer. Each test group of amputees comprised ten individuals of the same sex. Preliminary tests were made to determine if the amputations had any undesirable effect on general activity and on subsequent responses to humidity. Because, as will be shown below, surgery did not appear to produce any deleterious effects, all regular tests were begun 24 hours after amputation. The humidity reactions of each group of amputees were tested at least five times over a four-day period following amputation.

[1]Contribution No. 24, Canada Department of Agriculture Research Station, Saskatoon, Saskatchewan, in part from a thesis submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy at the University of Illinois, 1954.

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Results

Type and Structure of Antennal Sensilla

Sensilla belonging to four groups, classified according to Snodgrass (15), were observed: (a) *sensilla coeloconica*, or pit-peg organs, (b) *sensilla basiconica*, or peg organs, (c) *sensilla ampullacea*, or pouch-peg organs, and (d) *sensilla trichoidea* and *sensilla chaetica*, termed sensory setae in this paper.

Sensilla Coeloconica.—These organs (Fig. 1) are thin-walled, six to 11 microns in length, and four to five microns in diameter at the base. The oval sclerotized pit, 13 to 17 microns in diameter, has a dome-shaped cover with a spherical or oval opening near the apex. In most sensilla the peg is on the wall of the pit and leans toward the centre with the conical apex pointing toward the opening in the dome (Fig. 2). The base of the peg is heavily sclerotized and appears to be continuous with the wall of the pit (Fig. 3). Small piles of "debris" (12) are frequently found around the base of the peg within the pit.

Each of the coeloconic sensilla contains a single sense cell (Fig. 11, 12). Where the sensilla occur in clusters within the cuticulum of the antennae, the sense cells appear to be grouped by the anastomosis of their axons into a single nerve joined to the antennal nerve (Fig. 12).

Sensilla Basiconica.—Three distinct types are evident: (a) short and cone-shaped with a sclerotized basal ring (Fig. 4); (b) short and thorn-shaped without a basal ring (Fig. 5); and (c) trichoid-like with a doughnut-shaped basal ring (Fig. 6). These sensilla, which are 14 to 22 microns long, are approximately twice as long as the coeloconic sensilla. They also are thin-walled and each contains a group of sense cells (Fig. 13). These are described by Slifer (14).

Sensilla Ampullacea.—These structures are extremely rare on the antennae of *M. bivittatus*. The pouch in which the tiny sensillum is located is merely an invagination of the antennal cuticulum (Fig. 7). The sensilla, about four microns in length, are approximately half the size of the coeloconic sensilla. They appeared sclerotized throughout. No lumina were detected. Only two of these sensilla were found, and no nerves or sensory structures were detected.

Sensilla Trichoidea.—One or more long, slender, filamentous, setiform processes, 140 to 200 microns in length, are always present either on the scape or on the pedicel or on both. These are usually not freely moveable at the base (Fig. 8). The hair socket is usually flush with the surface of the cuticulum or is slightly elevated. A very thin or narrow lumen suggests a very heavy sclerotization of the setae.

Sensilla Chaetica.—These structures are found on all segments of the antennae. They are 26 to 34 microns in length and are usually heavily sclerotized. Some are connected to the sclerotized ring, which is above the general level of the antennal cuticulum, by a narrow basal membrane (Fig. 10) and thus are apparently moveable. The others are immovably set in an expanded sclerotized basal ring which is more or less flush with the cuticulum (Fig. 9). The sensilla chaetica and the sensilla trichoidea appear to be innervated by multiple sense cells similar to those innervating the sensilla basiconica.

Number and Distribution of Sensilla

No coeloconic sensilla were found on the three basal antennal segments of the various ontogenetic stages of *M. bivittatus*. The average numbers found on the other segments were:

Stage	First	Second	Third	Fourth	Fifth	Adult ♀	Adult ♂
Segment 4	2	0	0	1	1	2	1
" 5	0	2	0	2	1	3	2
" 6	2	0	0	0	2	0	1
" 7	0	0	2	0	1	3	4
" 8	19	2	0	0	4	0	2
" 9	8	0	1	7	2	8	8
" 10	26	1	1	1	6	4	7
" 11	20	0	6	11	6	12	12
" 12	23	26	1	1	29	11	17
" 13	15	11	10	21	17	26	25
" 14		30	2	11	27	29	31
" 15		23	30	36	24	35	38
" 16		26	20	14	40	29	34
" 17		17	31	46	38	42	42
" 18			25	33	46	37	42
" 19			24	36	42	37	41
" 20			14	25	56	36	37
" 21				25	39	40	43
" 22				17	36	23	29
" 23					24	23	26
" 24					23	14	18
" 25						21	22
Total	115	138	167	287	455	435	482

Basiconic sensilla were more numerous than the coeloconic and more prevalent on the distal segments of the antennae. None were found on the five basal segments. The average numbers on the other segments were:

Stage	First	Second	Third	Fourth	Fifth	Adult ♀	Adult ♂
Segment 6	1	0	0	0	0	0	0
" 7	1	0	0	0	0	0	1
" 8	37	0	0	0	1	0	2
" 9	28	0	0	2	1	3	12
" 10	43	0	0	1	5	11	21
" 11	32	0	7	13	16	24	43
" 12	38	42	1	8	32	44	63
" 13	27	41	13	31	35	71	77
" 14		44	1	24	49	62	79
" 15		30	44	38	64	74	79
" 16		43	46	36	62	87	82
" 17		24	46	62	58	91	81
" 18			34	58	62	85	63
" 19			42	51	67	96	68
" 20			23	31	76	80	53
" 21				39	67	80	57
" 22				23	52	76	48
" 23					37	58	38
" 24					41	32	20
" 25						46	33
Total	207	224	257	417	725	1020	920

'Sensory setae' were generally evenly distributed over the entire length of the antennae except that the adults had a preponderance on the scape and pedicel. The average numbers were:

Stage	First	Second	Third	Fourth	Fifth	Adult ♀	Adult ♂
Scape	5	5	6	12	12	64	49
Pedicel	6	5	7	10	11	38	39
Segment 3	7	4	6	9	8	8	5
" 4	5	3	6	8	8	8	5
" 5	6	4	8	11	8	10	7
" 6	8	5	7	6	8	11	6
" 7	10	3	5	7	9	10	9
" 8	11	6	7	8	12	13	12
" 9	9	4	8	12	13	14	15
" 10	9	6	7	13	16	19	18
" 11	8	3	11	14	18	20	19
" 12	9	6	9	16	19	23	22
" 13	8	8	10	16	19	22	20
" 14		6	11	18	19	23	23
" 15		6	12	15	18	23	23
" 16		6	11	16	20	20	21
" 17		7	10	14	18	21	21
" 18			9	14	17	19	21
" 19			7	12	16	20	21
" 20			8	10	15	19	19
" 21				9	12	18	20
" 22				13	13	17	17
" 23					10	13	16
" 24					18	11	13
" 25						32	33
Totals	101	87	165	263	337	496	474

Effects of Amputations

The humidity reactions of amputee grasshoppers did not vary significantly during the four-day period following surgery (Table I) indicating that antennectomies and palpectomies *per se* did not cause trauma, shock or other excision effects. The standard deviation of these tests was lower than in similar tests of normal grasshoppers (10).

The removal of the maxillary or of the labial palpi, or of both, did not reduce the response to humidity (Table II). The removal of the distal 15 segments of one antenna decreased the humidity response about 50 per cent, from a normal of 23 to 10 per cent. Removal of one entire antenna gave no greater reduction in reaction. The response to humidity was eliminated when the distal 15 seg-

TABLE I.

Effects of Surgery on the Reactions of *Melanoplus bivittatus* (Say) to a Choice Between 0 and 90 Per Cent Relative Humidity.

Amputation	Sex	No. of tests	Hrs. after amputation	Index of reaction* ±S.D.
Half antenna.....	male	9	3 to 77	9.3 ± 2.1
Half antenna.....	female	8	2 to 58	8.5 ± 2.0
Both antennae.....	male	8	11 to 83	0.6 ± 2.3
Labial palpi.....	female	8	4 to 78	24.6 ± 3.4

*The mean excess percentage of grasshoppers that preferred 0 to 90 per cent relative humidity.

TABLE II.

Effects of Antennal and Palpal Amputations on the Reactions of Adults of *Melanoplus bivittatus* (Say) to a Choice Between 0 and 90 Per Cent Relative Humidity

Number of segments amputated				Index of react'on* ±S.D.	
Labial palpi	Maxillary palpi	Right antenna	Left antenna	Females	Males
0	0	0	0	23 ± 4.9	26 ± 4.8
all	0	0	0	—	25 ± 3.6
all	all	0	0	—	23 ± 3.6
0	0	15	0	10 ± 2.1	10 ± 2.3
0	0	25	0	12 ± 3.0	—
0	all	25	0	10 ± 1.5	—
all	all	15	0	—	11 ± 1.9
all	all	25	0	—	11 ± 1.5
0	0	15	15	1 ± 1.6	2 ± 2.8
0	0	25	15	− 1 ± 1.2	− 0.2 ± 1.3
0	0	25	25	− 0.8 ± 1.5	0.6 ± 1.0
0	all	25	15	0.4 ± 1.9	—
0	all	25	25	0.4 ± 1.7	− 0.2 ± 0.1
all	all	25	15	1 ± 1.1	− 1 ± 2.2
all	all	25	25	0.4 ± 1.1	1 ± 1.8

*The mean excess percentage of grasshoppers that preferred 0 to 90 per cent relative humidity.

ments of both antennae were amputated, when these segments were removed from one antenna in the absence of the other, or when both antennae were excised.

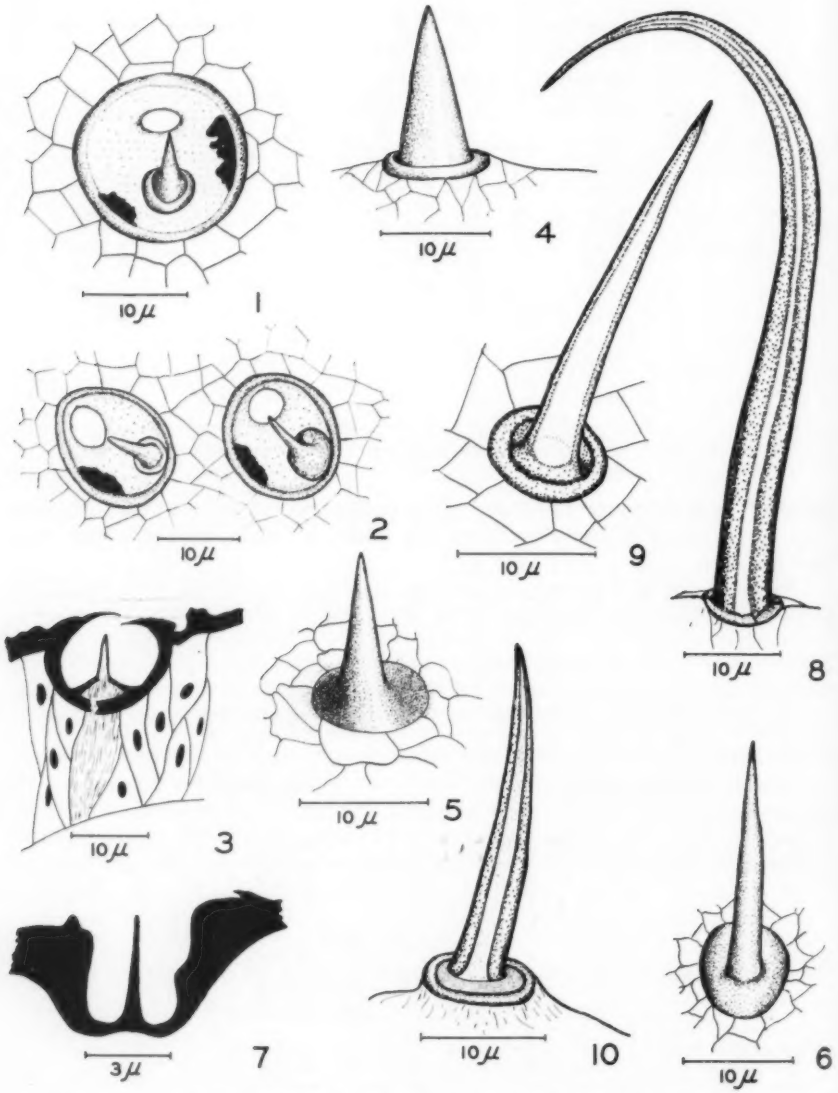
Progressively bi-segmental amputation of one or both antennae reduced progressively the humidity response of *M. bivittatus* (Table III). No reaction to

TABLE III.

Effects of Symmetrical and Asymmetrical Antennectomies on the Reactions of Adults of *Melanoplus bivittatus* (Say) to a Choice Between 0 and 90 Per Cent Relative Humidity

Segments removed		Index of reaction* ±S.D.	
Right antenna	Left antenna	Females	Males
0	0	23 ± 4.9	26 ± 4.8
2	0	17 ± 3.6	22 ± 1.9
2	2	—	13 ± 2.1
4	0	14 ± 3.9	16 ± 3.8
2	4	12 ± 1.5	—
4	4	—	10 ± 1.9
6	0	12 ± 2.9	12 ± 2.3
4	6	10 ± 1.7	—
6	6	—	8 ± 3.1
8	0	9 ± 1.1	11 ± 3.2
6	8	6 ± 1.6	—
8	8	—	0 ± 1.0
8	10	− 0.2 ± 1.1	—
10	0	—	10 ± 3.8
12	0	—	11 ± 1.5
12	2	—	8 ± 1.8
12	4	—	6 ± 3.3
12	6	—	3 ± 1.6
12	8	—	− 0.2 ± 2.4

*The mean excess percentage of grasshoppers that preferred 0 to 90 per cent relative humidity.



Figures 1 to 10: 1, 2, sensilla coeloconica, surface view; 3, sensillum coeloconicum, cross section; 4, 5, 6, sensilla basiconica; 7, sensillum ampullaceum, cross section; 8, sensillum trichoideum; 9, 10, sensilla chaetica.

TABLE IV.

Percentages of Functional Sensilla Remaining, and Reactions to a Choice of 0 and 90 Per Cent Relative Humidity, When Females of *Melanoplus bivittatus* (Say) were Subjected to Various Antennectomies.

No. of antennal segments removed		% of sensilla coeloconica remaining	% of sensilla basiconica remaining	% of sensory setae remaining	Index of reaction* ±S.D.
Right	Left				
0	0	100.0	100.0	100.0	23 ± 4.9
2	0	96.0	96.2	95.7	17 ± 3.6
4	0	90.7	89.6	92.6	14 ± 3.9
2	4	86.7	85.8	88.3	12 ± 1.5
6	0	82.0	81.8	88.9	12 ± 2.9
8	0	73.4	72.9	85.0	9 ± 1.1
4	6	72.6	71.4	81.6	10 ± 1.7
6	8	55.4	54.7	73.9	6 ± 1.6
25	0	50.0	50.0	50.0	12 ± 3.0
8	10	38.7	37.1	65.8	− 0.2 ± 1.1
15	15	4.6	1.4	39.3	1 ± 1.6
25	15	2.3	0.7	19.7	− 1 ± 1.2
25	25	0.0	0.0	0.0	− 0.8 ± 1.5

*The mean excess percentage of grasshoppers that preferred 0 to 90 per cent relative humidity.

humidity was shown after eight or more of the distal segments of both antennae were removed.

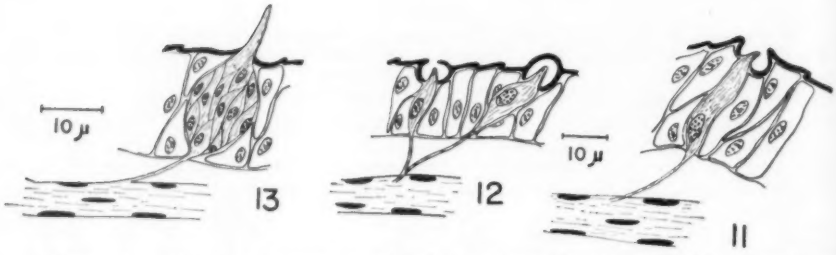
The distal eight segments of the antennae carried 48 per cent of the coeloconic and 54 per cent of the basiconic sensilla in females (Table IV), and 53 per cent of the coeloconic and 41 per cent of the basiconic sensilla in males (Table V). Thus, the removal of the eight distal segments of the antennae

TABLE V.

Percentages of Functional Sensilla Remaining, and Reactions to a Choice of 0 and 90 Per Cent Relative Humidity, When Males of *Melanoplus bivittatus* (Say) were Subjected to Various Antennectomies.

No. of antennal segments removed		% of sensilla coeloconica remaining	% of sensilla basiconica remaining	% of senory setae remaining	Index of reaction* ±S.D.
Right	Left				
0	0	100.0	100.0	100.0	26 ± 4.8
2	0	95.9	97.1	95.1	22 ± 1.9
2	2	91.7	94.2	90.3	13 ± 2.1
4	0	90.1	92.4	91.7	16 ± 3.8
6	0	81.8	86.5	87.6	12 ± 2.3
4	4	80.3	84.9	83.3	10 ± 1.9
8	0	73.2	79.3	83.1	11 ± 1.5
10	0	65.4	70.5	78.7	10 ± 3.8
6	6	63.7	72.9	75.1	8 ± 3.1
12	0	58.2	61.9	73.8	11 ± 3.2
12	2	54.0	59.0	69.0	8 ± 1.8
15	0	52.6	52.0	67.4	10 ± 2.3
12	4	48.3	54.3	65.5	6 ± 3.3
8	8	46.5	58.7	66.2	0 ± 1.0
12	6	40.0	48.4	61.4	3 ± 1.6
12	8	31.4	41.2	57.0	− 0.2 ± 2.4
15	15	5.2	3.9	34.8	2 ± 2.8
25	15	2.6	2.0	17.4	− 0.2 ± 1.3
25	25	0.0	0.0	0.0	0.6 ± 1.0

*The mean excess percentage of grasshoppers that preferred 0 to 90 per cent relative humidity.



Figures 11 to 13: 11, 12, innervation of sensilla coeloconica; 13, innervation of sensillum basiconicum.

removed about 50 per cent of the thin-walled sensilla and thereby eliminated completely the humidity reaction of the grasshoppers.

Discussion

The numbers of coeloconic sensilla on the antennae of the first instar nymphs and adults of *M. bivittatus* correspond almost exactly with those reported for the Moroccan Locust, *Dociostaurus maroccanus* (Thunb.) (4). Furthermore, the size of these sensilla and their distribution on the various segments of the antennae are nearly identical in these two species, which are widely separated geographically and differ greatly in habit.

Slifer (12) concluded that the thin-walled coeloconic and basiconic sensilla were hygro-receptive because, in *M. differentialis*, both types were quite permeable to dyes. Later she proved that the basiconic pegs on the antennae of *M. m. mexicanus* did not function as hygro-receptors although freely permeable to dyes (13). The humidity reactions of *M. bivittatus* that had undergone a series of antennal amputations suggest that the coeloconic sensilla of this closely related species function as hygro-receptors. Presumably the basiconic sensilla function as chemo-receptors.

The thick-walled 'sensory setae' are unlikely to be hygro-receptors because of the resistance offered by the heavily sclerotized cuticular layer and because they are impermeable to dyes (12). Many of these are moveable and may be classed as mechano-receptors. A great number are massed on the terminal segments of the antennal flagellum and are probably tactile in function.

When the eight distal segments of both antennae of adult *M. bivittatus* were excised, leaving 47 per cent of the 482 coeloconic sensilla, the insects did not react to humidity. It is interesting to note, however, that the first three nymphal instars, with 115, 138 and 167 sensilla, respectively, responded to humidity stimuli. Apparently the adults of *M. bivittatus*, like mealworm larvae (8) require a minimum number of operative sensilla to respond to hygrometric changes.

Summary

The type, structure and distribution of sense organs on the antennae of the two-striped grasshopper, *M. bivittatus*, were studied. Three major types of sensilla were observed and described: 1. *Sensilla coeloconica*, or pit-peg organs, 6 to 11 μ in length. 2. *Sensilla basiconica*, or peg organs, 14 to 22 μ in length. 3. *Sensilla trichoidea* and *Sensilla chaetica*, or sensory setae, 140 to 200 μ and 26 to 34 μ in length, respectively. A fourth type, *sensilla ampullacea*, or pouch-peg organ, measuring four microns in length is rarely present. Only two were observed during the investigation.

The number of antennal sensilla increased progressively as the post-embryological development of the insects advanced. The number of coeloconic sensilla increased from 115 in the first instar nymph to 482 in the adult; the basiconic sensilla increased from 207 to 1,020; and the 'sensory setae' increased from 100 to 496.

The coeloconic and basiconic sensilla were fairly equally distributed over the distal two-thirds of the antennal segments. Sensory setae were present on all segments. In adult grasshoppers most of these were present on the scape, the pedicel, and the terminal segment.

Hygro-reception is apparently the function of the coeloconic sensilla. Their thin walls allow penetration of moisture. Serial removal of antennal segments from the distal end, with consequent decrease in the number of functional sensilla, resulted in a progressive reduction in the intensity of the response to humidity changes. Removal of one half of the sensilla produced a complete elimination of the humidity reaction. This suggests that the hygro-response is the result of the combined stimulation of at least half of the coeloconic sensilla.

It is presumed that the thin-walled basiconic sensilla function as chemoreceptors (Slifer, 2). Because of their thick walls the 'sensory setae' were presumed to have a tactile or mechano-receptive function.

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A New Species of *Mecomma* Fieber from Canada, with Reference to *M. mimetica* Carv. and South. and *M. dispar* (Boh.) in North America (Hemiptera: Miridae)

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Carvalho and Southwood (1955) made a world revision of the *Cyrtorhinus-Mecomma* complex, and listed 11 species and three subspecies of *Mecomma.* Those reported from North America are: *ambulans* (Fall.), *gilvipes* (Stål), *luctuosa* (Prov.), *luctuosa pacifica* Carv. and South., *antennata* Van D., and *mimetica* Carv. and South.

In the present paper, *Mecomma bradora*, n.sp., is described from Quebec, and the distinguishing external and genitalic characters are given. Additional notes on the habits, morphology, and distribution of *Mecomma mimetica* are given, and the status of *Mecomma dispar* (Boheman) in North America is discussed.

Mecomma mimetica Carvalho and Southwood, 1955

Figs. 1-5

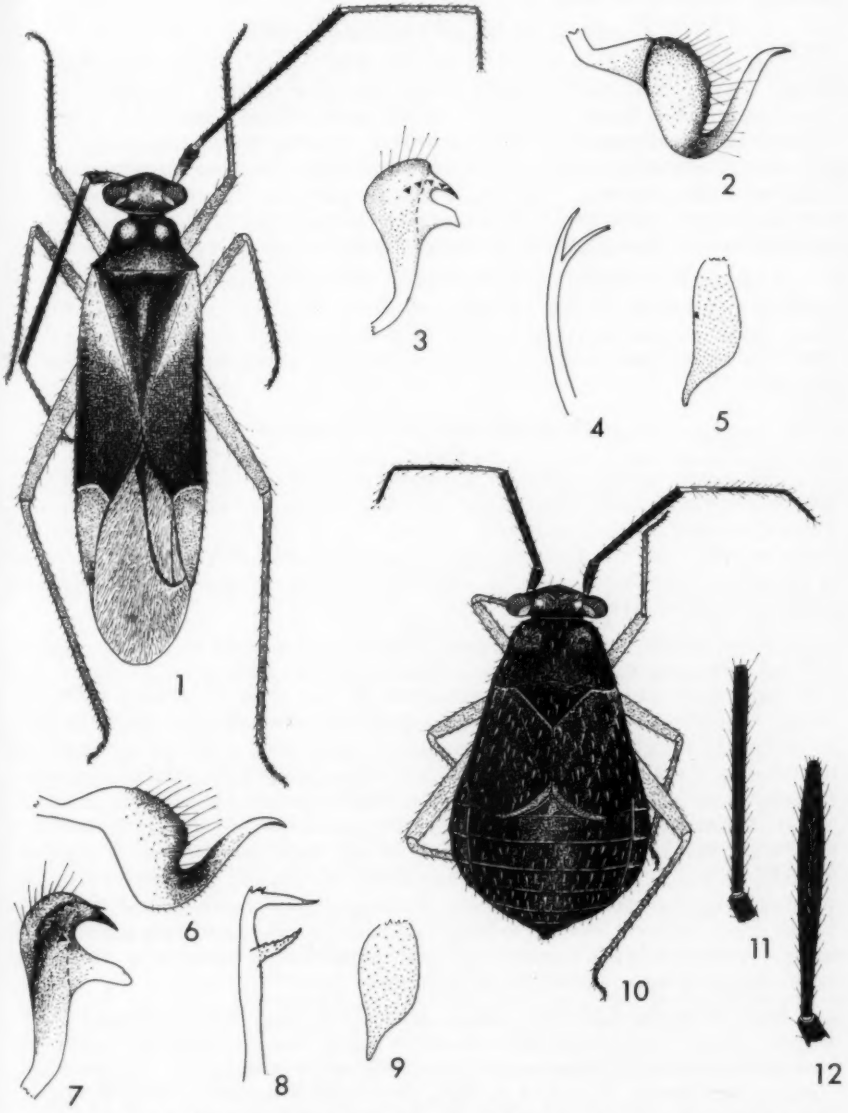
The species was originally described from a pair of females collected in British Columbia by Professor G. J. Spencer. The female was illustrated by Carvalho and Southwood.

This species differs markedly from the other *Mecomma* in the shape of the head and pronotum, and the clubbed second antennal segment of the females. The head is strongly rounded, and the calli of pronotum are raised and very prominent, forming a groove between them. There are thus very good external characters to separate *mimetica* from the other *Mecomma*, however, the male and female genital structures are very characteristic and place the species in *Mecomma.*

The strongly clavate second antennal segment is characteristic only of the female, that of the male is linear. As far as is known, the males are macropterous, while the females are both macropterous and brachypterous.

The writer collected the nymphs and adults on grasses in damp and shaded situations. The earliest collecting data on hand are for June 18, and the latest for September 4. The species appear to be transcontinental in temperate North America.

Distribution:—Alberta: Canmore, Drumheller, Edmonton, and Elkwater. British Columbia: Atlin, Cariboo, Hedley, Hope Mts., Kamloops, Merritt, Nicola, Osoyoos, Quesnel, Salt Spring Island, and Soda Creek. Colorado: Glen Haven, Little Beaver, and Pingree Park. Manitoba: Brandon, and Victoria



Figs. 1-12. 1-5, *Mecomma mimetica* Carvalho and Southwood; 6-11, *M. bradora* n.sp.; 12, *M. ambulans* (Fall.). 1, Adult, male; 2, 6, left clasper; 3, 7, right clasper; 4, 8, sp culum of the vesica; 5, 9, K structure of bursa copulatrix; 10, adult, female; 11, 12, second antennal segment of female.

Beach. New Hampshire: Glen House. North West Territories: Norman Wells. Ontario: Parry Sound. Quebec: Laniel, and Mt. Albert. Wyoming: Laramie. Yukon: Dawson.

Mecomma dispar (Boheman, 1852)

This species was recorded from the Nearctic region as *Globiceps dispar* by Knight (1922, 1923, 1927a, 1927b) and Blatchley (1926). Southwood and Woodroffe (1957) transferred *dispar* to *Mecomma* on the basis of the genitalia. This transfer was supported by Kelton (1959). During the present study, North American specimens labeled as *dispar* were compared to those of *mimetica* and found to be identical both externally and in the genitalia. There is thus evidence that *Mecomma dispar* (Boh.) does not occur in the Nearctic region, and former records of this species should be considered as *Mecomma mimetica* Carv. & South.

M. dispar and *mimetica* are very closely related but may be separated by the genitalia and colour pattern. Females of *dispar* have the second antennal segment black, whereas in *memetica* the basal half is pale. Males of *dispar* have relatively shorter and more incrassate second antennal segment than do those of *mimetica*.

Mecomma bradora, new species

Figs. 6-11

This species is very similar to *Mecomma ambulans* (Fall.) and has been considered conspecific with that species (Walley, 1932; Carvalho and Southwood, 1955; Carvalho, 1958; and Kelton, 1959). Study of European specimens of *ambulans* show that the Canadian species are noticeably different externally and in the genital structures. All the males and females on hand are macropterous and brachypterous respectively.

Female:—Length, 2.52-2.94 mm. Head: width, 0.84-0.91 mm.; vertex, 0.35-0.4 mm.; length, 0.37-0.42 mm.; head black, two faint spots on vertex near eyes pale; frons reddish-black; pubescence silvery, erect, especially a row on vertex. Antenna: I, 0.31-0.38 mm. long, black; II, 0.84-0.99 mm., black; uniform in thickness; densely pubescent, some hairs longer than width of segment; III, 0.8-0.9 mm., dark-brown, basal one-fifth to one-quarter pale, thicker than apex, densely pubescent; IV, 0.38-0.42 mm., dark brown, pubescent. Rostrum 1.29-1.36 mm. long, reaching hind coxa. Pronotum 0.5-0.56 mm. long; 0.84-0.91 mm. wide; black, callosities flat, reddish brown; basal area somewhat rugulose. Scutellum black. Hemelytra short, extending just beyond third abdominal segment; black, small area at base pale. Pubescence on pronotum and hemelytra rather dense, suberect, silvery, in length exceeding thickness of first antennal segment. Abdomen black, connexivum pale, pubescent as hemelytra. Legs pale, coxae darker at bases. Genitalia as illustrated.

Male:—Length, 4.06-4.48. Head: width, 0.8 mm.; vertex, 0.33-0.35 mm.; length, 0.29-0.35 mm.; head dark brown to black, two pale spots on vertex near eyes almost obscured; pubescence as in the female. Antenna: I, 0.42 mm. long, dark reddish-brown; II, 1.27-1.29 mm., dark reddish-brown, densely pubescent; III, 1.19-1.22 mm. dark reddish-brown, pubescent, some hairs longer than others; IV, 0.38-0.48 mm., brown, pubescent. Rostrum 1.29-1.31 mm. long, reaching hind coxa. Pronotum 0.54-0.59 mm. long; 0.98-1.03 mm. wide; dark brown to black. Scutellum dark brown. Hemelytra light brown to fuscous, darker on clavus, and lighter on commissure and corium. Membrane fuscous, veins dark. Pubescence on pronotum and hemelytra dense, suberect, yellowish in colour. Abdomen dark brown, connexivum pale; pubescence as on hemelytra. Femora

and coxae pale yellowish, coxae darker at bases; tibiae and tarsi infuscated. Genitalia as illustrated.

Holotype:—Female, Bradore Bay, Quebec. August 4, 1930. W. J. Brown. No. 7152 in the Canadian National Collection of Insects, Ottawa.

Allotype:—Male, same data as for holotype.

Paratypes:—15 females and 26 males, Bradore Bay, Quebec, July 19, 1929, and July 12-August 9, 1930, W. J. Brown.

This species differs from *M. ambulans*, which it most closely resembles, by the linear and shorter second antennal segment, smaller pale area on the third antennal segment, and the dusky, bluish colour of the females. The females of *ambulans* have a spindle-shaped second antennal segment (Fig. 12), being 1.01-1.15 mm. long, nearly one-half of third antennal segment pale at base, and the very glossy appearance. The genitalia of both sexes are distinct.

Summary

Mecomma ambulans (Fall.) and *M. dispar* (Boh.) do not occur in North America and previous records for these species should refer to *M. bradora*, n.sp., and *M. mimetica* Carv. and South., respectively. *M. mimetica* differs markedly in external appearance from the other species of *Mecomma* but the genitalia are very similar. *M. bradora* is known only from Quebec while *mimetica* is widespread in temperate North America, formerly recorded as *Globiceps dispar* (Boheman).

Acknowledgments

I wish to express my thanks to the following for sending material for study: Mr. P. D. Ashlock, United States National Museum; Mr. R. J. Izzard, British Museum (Natural History); Dr. T. R. E. Southwood, Imperial College of Science and Technology; and Dr. G. G. E. Scudder, University of British Columbia.

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Mass Rearing of the Cabbage Maggot, *Hylemya brassicae* (Bouché) (Diptera: Anthomyiidae) in the Greenhouse[1]

By D. C. Read[2]

Large numbers of each of the stages of the cabbage maggot, *Hylemya brassicae* (Bouché), are often required for studies on biology or on biological or chemical control of the insect. A method has been reported by Sherwood and Pond (1954) for maintaining a colony for more than a year. The method described herein enables mass rearing of eggs, larvae and pupae and easy separation of any stage.

Details of Method

The eggs, larvae, and pupae were reared in galvanized-iron cylinders (Fig. 1), in which the water table was maintained at approximately 15 inches below the surface of the soil. Three cylinders were placed so that the tops extended through the bottom of the greenhouse bench into a rearing cage similar to that described by Sherwood and Pond (1954), and about six more cylinders were kept outside the cage. The original supply of puparia was obtained from rutabaga and cabbage fields and the insects were separated from the soil with a flotation separator (Read, 1958) and stored at 36° to 45° F.

When flies were required for rearing, the field-collected puparia were placed at a depth of about two inches in the soil in one of the cylinders under the rearing cage. The flies emerged in two to six weeks and were fed on sugar solution and water in saturated absorbent cotton in small beakers. For oviposition, a slice of rutabaga, approximately 3 x 3 x 2 inches, was placed in each of the remaining two cylinders under the rearing cage so that about half an inch of the slice projected above the soil.

For rearing larvae, the slices were replaced by freshly cut pieces of rutabaga at three-day intervals. Those from the rearing cage were placed in a tray of sandy loam soil containing not more than about six per cent moisture to allow any fungus developing on the surface to die off. After six or seven days, the top inch of each infested slice was cut away and the remainder was placed on top of a fresh slice of rutabaga, 2½ x 2½ x ½ inches, in a cylinder of soil outside the rearing cage. At three-day intervals, fresh, half-inch slices were placed directly beneath the others in the cylinders and, as the larvae moved down from one slice to another, the top ones were discarded. This procedure was repeated until the larvae had matured and moved down into the soil to pupate. If sufficient food was not always available, larvae would move down into the soil and form puparia prematurely. To prevent this, 1½-inch cubes of rutabaga were kept at a depth of about seven inches in the soil in the centres of the cylinders. The cubes were replaced at weekly intervals and the infested ones were moved up to the tops of the cylinders. Eight of the cylinders (Fig. 1) were sufficient for rearing about 10,000 larvae or pupae.

For bioassay or other studies, immature larvae were obtained from infested slices of rutabaga that contained the stage desired, and mature larvae, puparia ted larvae, or newly pupated specimens were picked up with forceps from the upper eight inches of soil in a cylinder. The required number of specimens were picked from the soil with forceps, the soil then being replaced in the cylinder. *H. brassicae* are highly sensitive to any change in environmental conditions during

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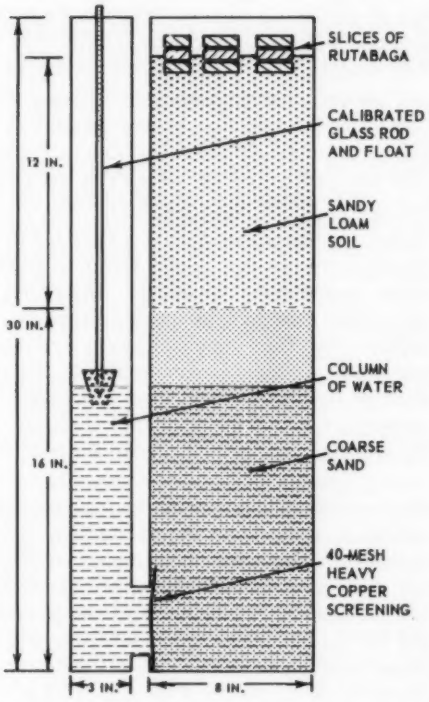

Fig. 1. Cut-away diagram of a galvanized-iron cylinder set up for rearing *H. brassicae*. The soil was first sifted through a 6-mesh sieve. The coarse sand was sifted through a 16-mesh sieve, and then washed repeatedly in a tub until all debris and fine particles had floated off. Both the sand and the soil were sterilized at 230° F. and 10 lb. pressure for two hours before being placed in the cylinders.

transformation from larva to pupa, and mature larvae or prepupae should not be washed or mechanically sifted from the soil in the cylinders.

If a second generation of flies was desired, the puparia were left in the soil and cheesecloth cages placed over the cylinders to prevent the emerging adults from escaping. If the insects were to be stored for future use, infested slices of rutabaga were removed, the cylinder was left undisturbed for at least seven days (so that all of the larvae had fully pupated); the upper 11-inch layer of soil was then sifted, and the puparia were collected and stored at below 50° F. to prolong development.

The temperature of the soil in the cylinders was maintained at between 60° and 65° F. and that of the rearing cage between 60° and 75° F. The relative humidity in the cage ranged from 40 to about 60 per cent. Although the higher levels favoured oviposition, reproduction was always high and control of humidity was not considered important.

Discussion

An estimated 5,000 larvae, puparia, or adults were reared per 100 female flies, and when the conditions described above for rearing the eggs, larvae, and pupae were provided, the insect reproduced very readily in the greenhouse.

More than 75 per cent of the larvae pupated between four and eight inches deep in the cylinders, where the moisture content of the soil was approximately 15 to 20 per cent (normal moisture capacity of the soil used was about 27 per cent).

For formation of puparia and pupation a relatively high soil moisture is evidently necessary, and, possibly because of the abrasive action of sand on the larvae, it is preferable to use a sandy loam soil in the rearing cylinders. Also, since the prepupae are apparently highly susceptible to attack by fungi, mites, and nematodes, it is advisable to use only sterilized soil.

Sherwood and Pond (1954) reported that a fluctuating temperature of 60° to 80° F. favoured emergence, and that adults failed to emerge when the pupae were held at a constant temperature of 60° F. However, during the present studies, emergence of adults from pupae ceased at about 70° F. When the temperature of the soil in which the larvae and pupae were reared was maintained at 60° F. adults emerged 20 to 40 days after pupation, the percentage mortality being much lower than at higher temperatures. Because of the high mortality at the higher temperatures, it was concluded that if the temperature was raised above 70° F., possibly to break diapause, it should be only for a short period of time.

Starting with adults, a new generation of flies was produced in 40 to 50 days at 60° to 65° F., and in approximately 75 days at 55° F. If large numbers (2,000 or more) of first-, second- or third-instar larvae were required for a bioassay or other test, the infested slices of rutabaga taken from the cylinders in the rearing cage over a period of two or three weeks were placed consecutively in cylinders of soil at 45°, 50°, and 55° F., so that all of the larvae would be at the same stage of development at the same time.

Acknowledgment

The author wishes to thank Mr. C. P. Duffy, Assistant Technician, for assistance throughout the study.

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Corrigendum

In the article "Hibernation Sites of Phytoseiids (Acarina: Phytoseiidae) in Ontario Peach Orchards", by Wm. L. Putman, Vol. 91, No. 11, November, 1959, in the table on page 739, "*T elongatus*" should read "*T. guatematensis*".

Microbial Isolations from the Granary Weevil *Sitophilus granarius* (L.) (Coleoptera: Curculionidae)

By R. E. CRAWFORD[1], L. A. MCDERMOTT[2], AND A. J. MUSGRAVE[3]

Introduction

The micro-organisms that accur in insects may be pathogenic, nonpathogenic, supposedly or actually beneficial, or casual invaders. The literature on the various aspects of the subject has become extensive (Buchner, 1953; Fraenkel, 1952; Shrewsbury and Barson, 1954a, 1954b; Steinhaus, 1946, 1949).

The granary weevil, *Sitophilus granarius* (L.), has attracted the attention of a number of investigators (Musgrave and Miller, 1958) because it is one of the many species of insects that harbour in definite organs special micro-organisms supposedly or actually of benefit to the host insect. The organs harbouring these micro-organisms were given the name mycetomes by Sülc (Steinhaus, 1946). It seems reasonable, therefore, to call them mycetomal micro-organisms. The relationship existing between the *Sitophilus* weevils and their mycetomal micro-organisms is complex (Musgrave and Miller, 1958). There seem to be at least two microbiologically different strains of *Sitophilus granarius*: the GG strain in which mycetomal micro-organisms can nearly always be found, and the MW strain in which, as recognizable in the GG strain, mycetomal micro-organisms are rare or absent (Musgrave and Miller, 1956). These mycetomal micro-organisms have been the object of study for some years, but they have not as yet with certainty been isolated and cultivated *in vitro*. Nor has any study been made of the general bacterial flora of these weevils.

The present work was initiated, therefore, to investigate the microbial population in both the GG and MW strains of *S. granarius*. Apart from the general interest of this work, it seemed that it might eventually aid in the isolation of the mycetomal micro-organisms in this insect by indicating what micro-organisms might be expected as "contaminants" with mycetomal organisms. Then, too, there was the possibility that if a micro-organism was isolated from the GG strain but not from the MW strain of weevils, it might subsequently prove to be the mycetomal micro-organism in the former strain.

Materials and Methods

The weevils were reared in pint preserving bottles at approximately 27°C., and 76% relative humidity, on Genesee whole wheat which had been previously heated at 122°C., for 20 minutes to rid it of any extraneous natural insect infestation. Larvae, pupae and adults were examined. They were taken from two kinds of insect cultures: young cultures which had been set up some 20 days previously and in which there was little frass; and old cultures, set up at least 40 days previously, which were dirty with frass and husks and powder from the attacked wheat grains. Adult weevils were taken at random from the cultures, and larvae and pupae were obtained by splitting open the grains of wheat.

Wheat infusion broth and Bacto nutrient broth (Difco) were employed as primary culture media in the isolation of bacteria from the insects. The wheat infusion broth was prepared by adding 10% newly-ground Genesee whole wheat to distilled water, allowing the mixture to stand for 24 hours at 5°C., then passing it through filter paper. The filtrate was sterilized by passage through a Seitz filter and aseptically dispensed into sterile 10 x 75 mm. test tubes. The nutrient broth was dispensed into similar tubes, but was sterilized in the tubes

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by autoclaving at 122°C., for 20 minutes. Both broths were always incubated in the tubes for 48 hours at 27°C., before use to check their sterility. For subsequent isolation, purification, culture and study of the bacteria from the weevils, the two broth culture media were solidified by the addition of 1.5% Bacto agar (Difco). Each specimen of insect to be examined for internal micro-organisms was surface-sterilized by immersion in a 2000 p.p.m. solution of Hyamine 1622 (Rohm and Hass, Phil., Pa.) for 30 to 60 seconds. It was then subjected to two washings in sterile distilled water and placed in a test tube of one of the primary broth culture media. This tube was then incubated, under aerobic conditions only, at 27°C., for 48 hours to test the sterility of the medium and the exterior of the insect. Sterility was assumed to have been achieved if the broth in the tube remained clear, and, if such was the case, the insect specimen was aseptically crushed in the broth and incubated for another 48 hours at 27°C.

A total of 72 specimens of the weevil were examined for internal micro-organisms:

Three stages of insect: larva, pupa and adult	3
Three specimens of each stage, (3 x 3)	9
Two strains of weevil: GG and MW, (2 x 9)	18
Two kinds of insect cultures: young and old, (2 x 18)	36
Two kinds of primary broth media: nutrient and wheat broths, (2 x 36)	72

Controls, set up to check the sterility of the techniques, the equipment and the culture media, as well as the efficiency of the surface-sterilization of the insects examined, were elaborate and proved to be consistent.

Isolations of micro-organisms were made from the tubes containing the crushed insects by streaking a loopful of the contents of each tube onto the surface of the corresponding solid culture medium in Petri plates and incubating these at 27°C., for 48 hours under aerobic conditions. Purification of the cultures of bacteria so obtained was accomplished by repeated streaking on fresh Petri plates containing the appropriate solid culture medium. The resulting pure cultures were studied according to the methods outlined in the Manual of Microbiological Methods (1957) and following the procedures of these tests as outlined or in the modified forms as used by Evelyn (1960). The following characteristics of the bacterial isolates were thus determined: optimum growth temperature, form, arrangement, size, Gram reaction and motility of vegetative cells; presence of endospores; growth on agar stroke and in nutrient broth; agar colonies; action on gelatine, nitrate, starch, urea, Tween 40 (lipolysis), casein, litmus milk, sheep blood agar, arabinose, rhamnose, xylose, glucose, fructose, galactose, mannose, lactose, sucrose, maltose, trehalose, melibiose, cellobiose, raffinose, melezitose, inulin, glycerol, adonitol, mannitol, sorbitol, dulcitol, inositol, salicin and aesculin; production of hydrogen sulphide, acetylmethylcarbinol, indole, catalase and oxidase; utilization of sodium citrate and ammonium phosphate; and reaction to the methyl red test. No attempt was made to study the antigenic structure or serological relationships of the bacteria isolated. The nomenclature and system of classification employed in Bergey's Manual of Determinative Bacteriology (Breed, *et al.*, 1957) were followed in identifying the bacteria isolated from the weevils.

To obtain some idea of the numbers of bacteria in the environments of the weevils before and during their culture, bacterial plate counts were made of (a) the Genesee wheat after it was given its preliminary heating, but before it was used in culturing the weevils, (b) the wheat, frass, etc., in a jar of a young

culture of weevils some 20 days old, and (c) the wheat, frass, etc., in a jar of an old culture of weevils some 60 days old. Dilutions of the wheat, frass, etc., were made in sterile 0.1% peptone (Difco) in distilled water, and Bacto nutrient agar (Difco) was employed as the culture medium with an incubation temperature of 27°C., for 96 hours under aerobic conditions. No attempt was made to identify the bacteria obtained in making these counts. Macroscopically, however, they appeared to be of many different types. These determinations were made after the isolations of micro-organisms from the insects were finished, and the insect cultures employed were similar to, but were not the same cultures as those from which weevils had been removed for microbial examinations. However, the results obtained provide an approximate assessment of the microbial content of the environments in which the weevils lived.

Results

All controls were satisfactory. However, one tube containing a pupa from a new culture of the MW strain of weevil and crushed in Bacto nutrient broth became contaminated as a result of an accident during handling and was discarded. This left 71 specimens for examination.

Only three species of bacteria were isolated from the various stages of the *Sitophilus* weevils under the conditions of this investigation. These bacteria were identified as a species of the genus *Corynebacterium*, a member of the *Bacillus cereus* Frankland and Frankland group, and *Micrococcus freudenreichii* Guillebeau. Details of the isolations are given in Table I.

The numbers of bacteria associated with the wheat before its use as insect food, and the numbers of bacteria in the wheat, frass, etc., in new and old cultures of the weevils are shown in Table II.

Discussion

The wheat used in this investigation for rearing the weevils initially contained relatively few bacteria. Later, after weevils had been living in it, the bacterial count of the wheat increased several thousandfold. It may be assumed that the weevils used in the experiments were derived from environments of this kind. Thus, it is interesting that the insects themselves gave evidence of having a rather sparse bacterial flora. Indeed, only three species of bacteria were isolated from them. Somewhat similar conditions have been found in other insects, and various explanations have been offered (Bucher, 1959; Steinhaus, 1949).

It is of additional interest that in each isolation only one species of bacterium was obtained. The two culture media employed seemed equally acceptable to all three bacterial species isolated and are known to be capable of supporting the growth of a wide variety of micro-organisms. No Gram-negative bacteria were isolated from the weevils, although such bacteria are thought to be present in large numbers in various insects (Bucher and Stephens, 1959a, 1959b; Steinhaus, 1949).

Attention may be drawn to the fact that, while the frequency of the three bacterial species in the different strains and stages of the weevils was variable, nonetheless, a distribution pattern could be discerned. *Corynebacterium* sp. was isolated more often from strain GG than from strain MW of weevils, but was never isolated from the adults of either strain. *B. cereus* was isolated more often from adults than from larvae, more often from larvae than pupae, and with almost equal frequency from both strains. *M. freudenreichii* was isolated more often from pupae than from adults, and nearly twice as often from strain MW as from strain GG. At the present state of our knowledge, no significance can be

TABLE I

Bacteria Isolated from *Sitophilus granarius*

Strain	Insect Culture	Stage	Broth Culture Medium	Number of Times Bacteria Isolated		
				Corynebact. sp.	*B. cereus*	*M. freudenreichii*
GG	New	Larva	Nutrient	3	0	0
			Wheat	1	2	0
		Pupa	Nutrient	0	2	0
			Wheat	0	0	3
		Adult	Nutrient	0	3	0
			Wheat	0	3	0
	Old	Larva	Nutrient	0	2	1
			Wheat	0	1	2
		Pupa	Nutrient	1	0	2
			Wheat	3	0	0
		Adult	Nutrient	0	1	2
			Wheat	0	3	0
MW	New	Larva	Nutrient	1	0	2
			Wheat	0	3	0
		Pupa	Nutrient	0	2	1
			Wheat	0	0	3
		Adult	Nutrient	0	3	0
			Wheat	0	3	0
	Old	Larva	Nutrient	0	2	1
			Wheat	0	0	3
		Pupa	Nutrient	1	0	2
			Wheat	0	0	3
		Adult	Nutrient	0	2	1
			Wheat	0	0	3
Totals				10	32	29

TABLE II

Bacterial Count of Weevil Environments

Environment	Bacteria per Gram
Genesee wheat after heating and before use in insect cultures	Less than 500
Wheat, frass, etc., in new culture of insect	3,500,000
Wheat, frass, etc., in old culture of insect	800,000,000

attached to these distributions. However, the apparent absence of *Corynebacterium* sp. from adult weevils may be significant. Various species of *Corynebacterium*, members of the *B. cereus* group and *M. freudenreichii* have been reported isolated from various insects (Steinhaus, 1946).

There was no evidence that any of the three bacterial species was pathogenic to the weevils or that it was the one normally inhabiting the mycetome in the GG strain of weevils in great numbers.

Summary

Only three species of bacteria: *Corynebacterium* sp., a member of the *Bacillus cereus* Frankland and Frankland group, and *Micrococcus freudenreichii* Guillebeau were isolated from larva, pupa and adult stages of GG and MW strains of the granary weevil, *Sitophilus granarius* (L.). None of these bacteria was obviously pathogenic to the weevils, nor did any one of them seem to be the micro-organism normally inhabiting the mycetome in the GG strain in great numbers.

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Notes on the Volterra Equations

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According to one of the popular ecological theories, populations are self-governing systems, which maintain themselves in existence by utilizing "density-dependent factors",whose effect becomes more intense as the population increases and less intense as it decreases. This theory is connected with a mathematical model developed by V. A. Bailey and A. J. Nicholson, 1935, to represent the results of the interaction of predator and prey populations. According to the theory, as expressed verbally, a disturbance of the conditions of stability — the "steady state" — produces oscillations which tend to re-establish the stable condition. In fact, however, when numbers are inserted in the equations, the population values, at the end of one or more cycles — which increase in amplitude if there are more than one — fall below unity, which, on a common sense view may be considered to mean the extermination of the prey, followed by that of its predator or parasite.

It is true that in certain laboratory experiments the population curves of predator and prey correspond pretty well to those given by the Bailey-Nicholson equations. Nevertheless they do not appear in general to correspond to events in the field and they are especially inadequate in that they fail to show the maintenance in existence of the populations, which is, perhaps, what they are chiefly designed to illustrate and explain.

On the other hand, the Lotka-Volterra equations, which antedated the Bailey-Nicholson equations by a good many years and were very extensively developed by Volterra in a series of papers published from 1926 onward, do imply (at least within certain limits) the maintenance in existence of the population and do also illustrate some of the points particularly stressed by the Bailey-Nicholson school. A good example is the "law" of the disturbance of the mean population values. If, said Volterra, (1927, p. 24) one attempts to destroy uniformly and in proportion to their number, the individuals of the two species, the mean value of the host population rises, while that of the predator (or parasite) population falls.

The differential equations representing the interaction of a predator and its prey — for example, of an insect parasite and its host—were based on very simple assumptions. It may be convenient to recall them here.

Volterra considers the case of two species, one of which feeds on the other. Let N_1 and N_2 says Volterra, be the number of individuals of the two species. The coefficient of increase the first species (the prey or "host") would have if the other (the predator or parasite) were not present would be $\epsilon_1 > 0$. We may suppose that the second species (the predator or parasite) would die out for lack of food if it were alone. In that case, its "coefficient of increase" would be negative and would be $-\epsilon_2$, which is therefore a coefficient of decrease. If each of the species were alone, we would have

$$\frac{dN_1}{dt} = \epsilon_1 N_1 \quad \text{and} \quad \frac{dN_2}{dt} = -\epsilon_2 N_2.$$

But if they are associated and the second species feeds on the first, ϵ_1 will diminish and $-\epsilon_2$ will grow. The more abundant the parasite is, the more the value of ϵ_1 will fall and the more abundant the host, the more $-\epsilon_2$ will increase, that is to say, the less rapidly the parasite population will decline. There seems to be a little ambiguity here, but the meaning of Volterra's words is that the rate of extinction will become a rate of survival. To represent these ideas in the simplest manner, let us suppose that ϵ_1 diminishes in proportion to the value of N_2 and to an extent we designate as $\gamma_1 N_2$, while $-\epsilon_2$ increases in proportion to the value of N_1 and to an extent we designate as $\gamma_2 N_1$. We shall then have the two differential equations:

$$(1) \quad \frac{dN_1}{dt} = (\epsilon_1 - \gamma_1 N_2)N_1$$

$$(2) \quad \frac{dN_2}{dt} = (-\epsilon_2 + \gamma_2 N_1)N_2$$

giving the rates of change of the populations in relation to time.

To assume that the coefficients of increase and decrease with respect to N_2 and N_1 are respectively linear, said Volterra, may seem very crude but it is justified if we calculate these coefficients according to the probable number of encounters of the two species.

The biological interpretation of the coefficients γ_1 and γ_2 requires a little consideration. Volterra called γ_1 the coefficient of defence or the host species, γ_2 the coefficient of attack (or voracity) of the predator or parasite (1935, p. 26). He also called γ_1 the numerical measure of "l'attitudine a proteggersi" of the host species (1927) and this could reasonably be translated as the power of defence against the parasite. I feel, however, that this interpretation is incorrect, since it does not agree with the trends given by the equation. If we put $\epsilon_1 = 0.5$, $N_2 = 50$ and $\gamma_1 = 0.01$ in the equation for N_1, the right-hand side of the equation becomes zero, so that at this point the host population is stable, neither increasing or decreasing. If now we *increase* γ_1 to 0.1, the quantity within the brackets becomes $-4.5\ N_2$ and this shows that the population of the host is *falling*. If we *decrease* γ_1 giving it the value of 0.001, the quantity within the brackets becomes $+4.5\ N_2$ and this shows that the population of the host is *rising*. This means, if γ_1 measures the power of *defence*, that an *increase* in this power causes the host population to *fall* while a *decrease* in it causes the host population to *rise*. This is biologically inacceptable. I suggest, therefore, that γ_1 must be the *coefficient* of *accessibility* of the host with respect to the parasite. The idea of accessibility, as I have defined it elsewhere (1929, p. 462) refers, not only to the relation of host and parasite in space and time but also to the degree of specific attraction of one species for the other. A similar test made with γ_2 shows that when the value of this factor *rises*, the parasite population *rises*, when it *falls*, the parasite population *falls*, so it is correctly described as the coefficient of attack. A curious implication of the equations, which exists also in the Bailey-Nicholson formulations, and has been rightly criticized, is that while the rate of increase of the host is *limited*, having a maximum of ϵ_1, when there are *no* parasites, the rate of increase of the parasite is not but *will increase indefinitely* with the increase of the prey population. However, if numerical values are suitably chosen, this difficulty can be avoided.

The trends given by the Volterra equations, when numerical values are inserted, are easily determined. If the value of $\frac{dN_1}{dt}$ or $\frac{dN_2}{dt}$ is *positive*, the curve is *rising*; if it is *zero*, the curve is *stationary*; if it is *negative*, the curve is *falling*. Volterra showed, as had Lotka, that geometrical integration produces a "family" of closed curves, which have not, in general, a centre of symmetry, and we have therefore a periodic fluctuation. The period of these depends only on the values of ϵ_1, ϵ_2 and a constant. The averages of the two species are constant, for given values of ϵ_1, ϵ_2, γ_1 and γ_2, whatever be the initial values of N_1 and N_2. The average value of $N_1 = \frac{\epsilon_2}{\gamma_2}$; the average value of $N_2 = \frac{\epsilon_1}{\gamma_1}$. If the individuals of the two species are destroyed uniformly and in proportion to their numbers, the average of the prey (N_1) will rise and the average of the predator (N_2) will fall. Protecting the two species to the same extent, on the contrary, increases the averages of both (l.c. 1927, p. 25).

In order to integrate his equations analytically, Volterra simplified them by neglecting infinitesimals of the second order. The "family" of closed curves corresponding to the equations is then a system of concentric ellipses, having for centre the centre of fluctuation. Their period is not notably altered either by a change in the initial values of N_1 and N_2 or in the coefficients of accessibility and attack. The uniform destruction of individuals of N_2 accelerates the fluctuations while the destruction of individuals of N_1 slows them down. If individuals of the two species are contemporaneously and uniformly destroyed, the amplitude of the fluctuation of the host population will increase in relation to the amplitude of the fluctuation of the parasite population.

In the case of these small fluctuations, the amplitudes will be:

$$f_1 = 2E\frac{\gamma_1}{\sqrt{\epsilon_1}}, \quad f_2 = 2E\frac{\gamma_2}{\sqrt{\epsilon_2}}$$

and the relation between the amplitudes will be:

$$\frac{f_1}{f_2} = \frac{\gamma_1}{\gamma_2}\sqrt{\frac{\epsilon_2}{\epsilon_1}}$$

The period, in these cases, will be given by the formula:

$$\frac{2\pi}{\sqrt{\epsilon_1\epsilon_2}}$$

These generalizations, though of much interest, seem inadequate for ecological purposes, for various reasons. The lack of any reasonably handy methods for constructing the Volterra curves, with precise numerical values, is a serious inconvenience with respect to experimental and field tests. The object of this short paper is to describe and illustrate such methods. They will not be altogether novel to expert mathematicians, but experience suggests that many working entomologists may find them useful. Their publication does not imply that the biological theory they represent is regarded as valid. Nevertheless is it is of interest, and it may be that under certain circumstances it corresponds to certain series of events in the laboratory or in the field. It is unlikely that any particular mathematical model will be universally applicable.

The most reliable method of dealing with the Volterra equations is simply an application of the familiar Taylor theorem. This is a finite difference method but gives the effect of using infinitesimals, so that it applies to the equations as they were written. The two other methods are approximations, valid only within limits, but the calculations are much less labourious than those required by the Taylor series.

Taking first the integration by the Taylor series and denoting differentiation with respect to t by a superscript, we have:

$$\frac{dN_1}{dt} = N_1^{\,I}, \quad \frac{dN_2}{dt} = N_2^{\,I}$$

Taylor's theorem for an interval of 1/2 may then be written:—

$$N_1(1/2) = N_1(0) + (1/2)\frac{1}{1!}N_1^{\,I}(0) + (1/2)^2\frac{1}{2!}N_1^{\,II}(0) + (1/2)^3\frac{1}{3!}N_1^{\,III}(0) + (1/2)^4\frac{1}{4!}N_1^{\,IV}(0) +$$

$$(1/2)^5\frac{1}{5!}N_1^{\,V}(0) + \ldots$$

For an interval of (1) this simplifies to:—

$$N_1(1) = N_1(0) + N_1^{\,I}(0) + 0.5\,N_1^{\,II}(0) + 0.166\,N_1^{\,III}(0) + 0.0416\,N_1^{\,IV}(0) + 0.0083\,N_1^{\,V}(0) + \ldots$$

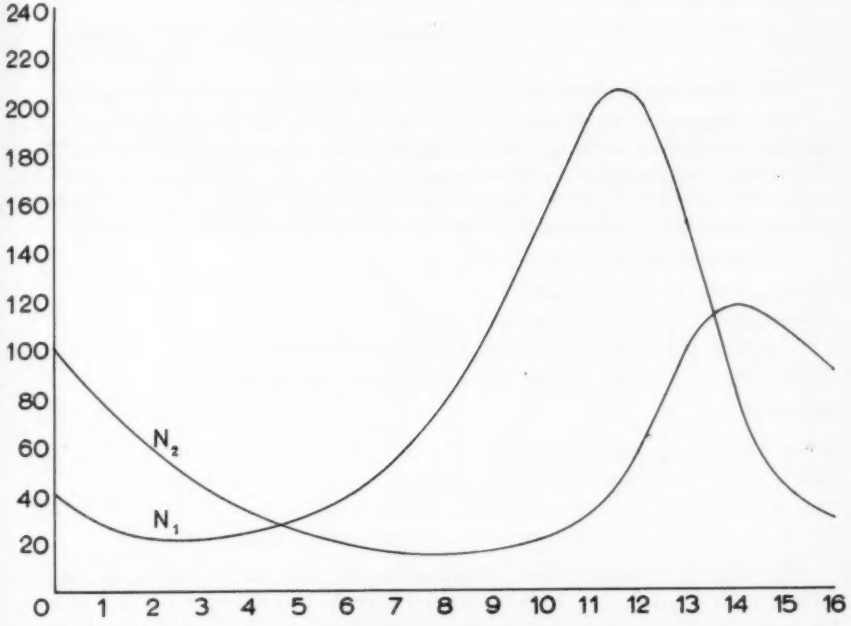

Fig. 1. Graph of Volterra equations where $N_1 = 40$, $N_2 = 100$, $\epsilon_1 = 0.5$, $\epsilon_2 = 0.4$, $\gamma_1 = 0.01$, $\gamma_2 = 0.005$; integration by Taylor theorem.

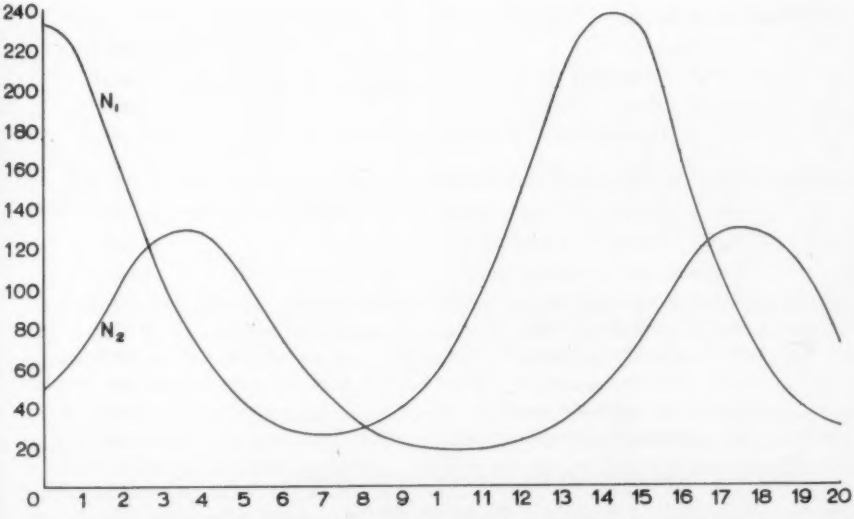

Fig. 2. Values as in Fig. 1; integration with equations (4) and (5).

This halves the number of operations but greater accuracy and a smoother curve may be obtained with the interval of (1/2), when we have:—

$$N_1(1/2) = N_1(0) + 0.5\,N_1^{I}(0) + 0.125\,N_1^{II}(0) + 0.02083\,N_1^{IX}(0) + 0.0026\,N_1^{IV}(0) + 0.00026\,N_1^{V}(0) + \ldots \quad (3)$$

Near the maxima or minima a smaller interval (e.g. 0.25) may be required.

The meaning of the theorem is that if the formulae for the second, third, fourth and fifth differentials of N_1 and N_2 are obtained (the equations (1) and (2) being the differentials) and multiplied by their respective coefficients, the total is the next point in the curve of N_1 or N_2 for the interval selected. In this case the successive differentials are obtained by following the usual rule for the differentiation of products.

The derivatives for N_1 and N_2 are:

$$N_1^{II} = \epsilon_1 N_1^{I} - \gamma_1 (N_1N^{I} + N_2N_1^{I})$$
$$N_1^{III} = \epsilon_1 N_1^{II} - \gamma_1 (N_1N_2^{II} + 2N_1^{I}N_2^{I} + N_1^{II}N_2)$$
$$N_1^{IV} = \epsilon_1 N_1^{III} - \gamma_1 (N_1N_1^{III} + 3N_1^{I}N_2^{II} + 3N_1^{II}N_2^{I} + N_1^{III}N_2)$$
$$N_1^{V} = \epsilon_1 N_1^{IV} - \gamma_1 (N_1N_2^{IV} + 4N_1^{I}N_2^{III} + 6N_1^{II}N_2^{II} + 4N_1^{III}N_2^{I} + N_1^{IV}N_2)$$

and for N_2:—

$$N_2^{II} = -\epsilon_2 N_2^{I} + \gamma_2 (N_1N_2^{I} + N_2N_1^{I})$$
$$N_2^{III} = -\epsilon_2 N_2^{II} + \gamma_2 (N_1N_2^{II} + 2N_1^{I}N_2^{I} + N_1^{II}N_2)$$
$$N_2^{IV} = -\epsilon_2 N_2^{III} + \gamma_2 (N_1N_2^{III} + 3N_1^{I}N_2^{II} + 3N_1^{II}N_2^{I} + N_1^{III}N_2)$$
$$N_2^{V} = -\epsilon_2 N_2^{IV} + \gamma_2 (N_1N_2^{IV} + 4N_1^{I}N_2^{III} + 6N_1N_2^{II} + 4N_1^{III}N_2^{I} + N_1^{IV}N_2)$$

Since the expressions within the brackets are the same for N_1 and N_2, we may call these T°, T^{I}, T^{II}, T^{III}, T^{IV}, T° being derived from the original equations and $= N_1N_2$, the equations may be simplified by substituting them and the T values need then be calculated only once for each pair of equations.

The values of ϵ and γ are taken as fractions of unity in the computations. Taking as an example,

$$N_1 = 100, \quad N_2 = 40, \quad \epsilon_1 = 0.5, \quad \epsilon_2 = 0.4, \quad \gamma_1 = 0.01, \quad \gamma_2 = 0.006,$$

we proceed as follows:—

$T^{\circ} = N_1N_2$	4000.000
$N_1^{I} = -0.01T^{\circ} + 0.5N_1$	10.000
$N_2^{I} = 0.006T^{\circ} - 0.4N_2$	8.000
$T^{I} = N_1N_2^{I} + N_2N_1^{I}$	1200.000
$N_1^{II} = -0.01T^{I} + 0.5N_1^{I}$	−7.000
$N_2^{II} = 0.006T^{I} - 0.4N_2^{I}$	4.000
$T^{II} = 2N_1^{I}N_2^{I} + N_1N_2^{II} + N_1^{II}N_2$	280.000
$N_1^{III} = -0.01T^{II} + 0.5N_1^{II}$	−6.300
$N_2^{III} = 0.006T^{II} - 0.4N_2^{II}$	0.080
$T^{III} = 3(N_1^{I} + N_2^{II} + N_1^{II}N_2^{I}) + N_1N_2^{III} + N_2N_1^{III}$	−292.000
$N_1^{IV} = -0.01T^{III} + 0.5N_1^{III}$	−0.200
$N_2^{IV} = 0.006T^{III} - 0.4N_2^{III}$	−1.800
$T^{IV} = 6N_1^{II}N_2^{II} + 4(N_1^{I}N_2^{III} + N_1^{III}N_2^{I}) + N_2N_1^{IV} + N_1N_2^{IV}$	−554.400
$N_1^{V} = -0.01T^{IV} + 0.5N_1^{IV}$	5.000
$N_2^{V} = 0.006T^{IV} - 0.4N_2^{IV}$	−3.000

Inserting these values in the equation (3) we obtain:

$$N_1(1/2) = 103.995$$
$$N_2(1/2) = 44.496$$

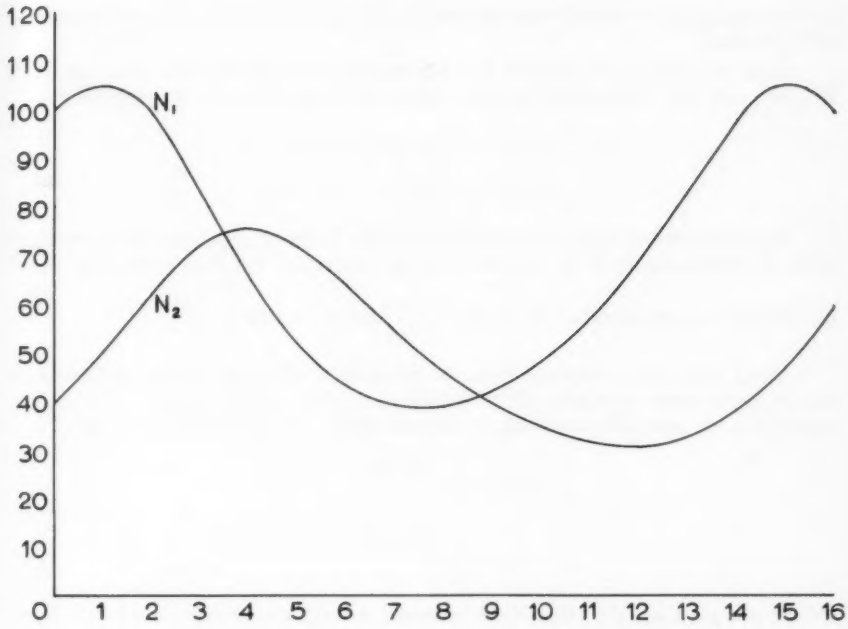

Fig. 3. $N_1 = 100$, $N_2 = 40$, $\alpha_1 = 0.5$, $\gamma_2 = 0.006$; integration by Taylor theorem.

With these values we repeat the process and eventually obtain

$$N_1(1) = 105.495$$
$$N_2(1) = 49.916$$

From the second step onward, the computation can be checked. According to Taylor's theorem we have:—

$$N(0) = \left\{N(1/2) + 0.125\ N^{II}(1/2) + 0.0026\ N^{IV}(1/2)\right\} - \left\{0.5\ N^{I} + 0.02083\ N^{III}(1/2) + 0.00026\ N^{V}(1/2)\right\}$$

The values for the derivatives are inserted and multiplied by their respective coefficients and we eventually get:—

$$N_1(0) = 100.0003$$
$$N_2(0) = 39.9995$$

which are very close to the original values. In fact, a difference of less than one integer may usually be regarded as satisfactory, If it is greater, an arithmetical error may be suspected and as the calculations are complex, errors can easily be made. The check is therefore necessary.

It may be worth while noting that if only the first derivatives are taken in the step by step integration, the amplitude of the oscillations increases in the successive cycles, as with the Bailey-Nicholson equations. Such an attempt at simplification removes the benefits of the method, which, as has been said, is the elimination of the effects of using finite steps. On the other hand, an increase of the interval fom 0.5 to 1 seems to have no serious effects except near the maxima or minima. A check back from the figure at 2,

for example, gives the initial value obtained by the check back from 1, when an interval of 0.5 is taken.

From the second step onward it is not necessary to calculate the exact values of T^{IV}, N_1^V, and N_2^V. Sufficiently accurate values of N^V are given by the equations:—

$$N^V(0.5) = 2\left\{N^{IV}(0.5) - N^{IV}(0)\right\}$$

$$N^V(1.0) = 2\left\{N^{IV}(1.0) - N^{IV}(0.5)\right\}$$

As already noted, approximate solutions of the Volterra equations can be produced when the infinitesimals of the second order are neglected. We then obtain the "small oscillations" that occur when N_1 nearly $= \frac{\epsilon_2}{\gamma_2}$, and N_2 nearly $= \frac{\epsilon_1}{\gamma_1}$.

Many years ago I obtained from the Scientific Computing Service in London, a pair of approximate solutions which I published in 1947, but the journal in which they appeared is not generally accessible to entomologists. The equations are as follows:—

$$N_1 = \frac{\epsilon_2}{\gamma_2} e^{A\cos pt} \tag{4}$$

$$N_2 = \frac{\epsilon_1}{\gamma_1} e^{B\sin pt} \tag{5}$$

Where $p = \sqrt{\epsilon_1\epsilon_2}$ and the value of the constants A and B can be calculated by the formulae:—

$$A = \sqrt{2\left[\log\frac{\epsilon_2}{\gamma_2} - \frac{1}{\epsilon_2}\left\{\epsilon_1 \log N_2 - \epsilon_2 \log N_1 - \gamma_1 N_2 - \gamma_2 N_1 + \epsilon_1\left(\log\frac{\gamma_1}{\epsilon_1} + 1\right)\right\} - 1\right]}$$

$$B = \sqrt{\frac{\epsilon_2}{\epsilon_1}}\,A.$$

With these equations t is reckoned from the point N_1 is a maximum. I found that the complex formula for A can be checked by using the principle that since the populations of N_1 and N_2 are stabilized when $N_1 = \frac{\epsilon_2}{\gamma_2}$, and $N_2 = \frac{\epsilon_1}{\gamma_1}$; this will be true for all values of t, when $A = 0$. Substituting this value in the equation, the right-hand side reduces to zero, as required. Similarly, numerical values of the stable conditions, e.g. $N_1 = 80$, $N_2 = 50$, $\epsilon_1 = 0.5$, $\epsilon_2 = 0.4$, $\gamma_1 = 0.01$, $\gamma_2 = 0.005$, make the value of $A = 0$.

Approximate solutions for the case of small oscillations were also published by Volterra (1926, p. 21). They are:—

$$N_1 = \frac{\epsilon_2}{\gamma_2} + \frac{\gamma_1}{\sqrt{\epsilon_1}} E\cos\left(\sqrt{\epsilon_1\epsilon_2}\,t + \alpha\right) \quad \left(\sqrt{\epsilon_1\epsilon_2}\,t + \alpha\right) \tag{6}$$

$$N_2 = \frac{\epsilon_1}{\gamma_1} + \frac{\gamma_2}{\sqrt{\epsilon_2}} E\sin\left(\sqrt{\epsilon_1\epsilon_2}\,t + \alpha\right) \tag{7}$$

If the equations are simplified by putting $\alpha = 0$, and the selected initial value of N_1 set at $t = 0$, E can be readily determined and then set in the equation for N_2. The computation is very simple.

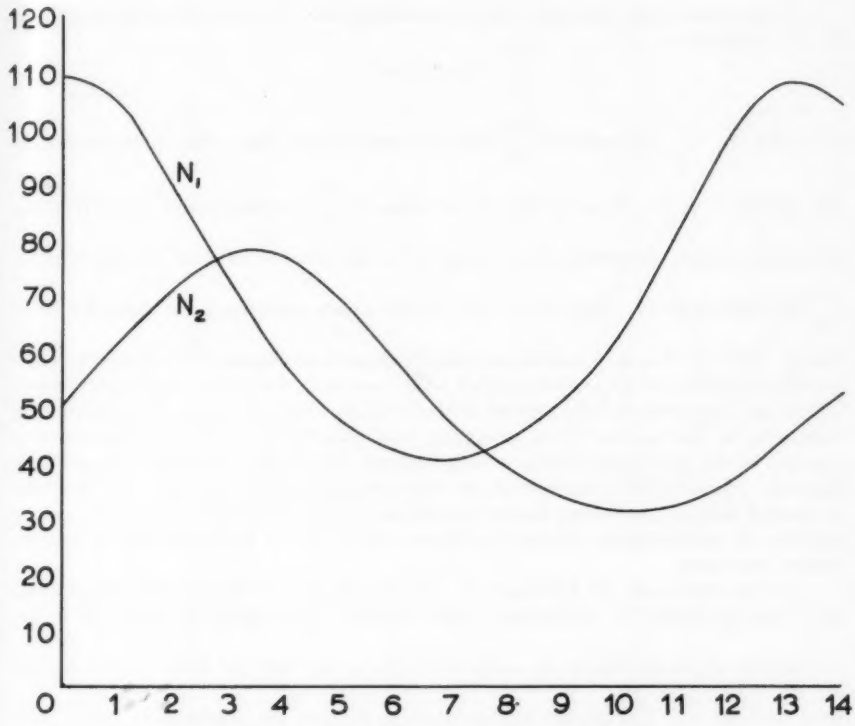

Fig. 4. Values as in Fig. 3; integration with equations (4) and (5).

It will be evident that the most reliable method of constructing the Volterra curves is the use of the Taylor theorem since it can be employed with any values of the constants. The smaller the interval, the longer the chain of differentials, the smoother the curve, but the more probable it is that arithmetical errors will creep in, misplaced decimals and change of sign being the most frequent. The method is laborious, at least with the facilities available to the writer.

As has been already noted, the values of N_1 and N_2 remain stationary when $N_1 = \frac{\epsilon_2}{\gamma_2}$, and $N_2 = \frac{\epsilon_1}{\gamma_1}$. If there is inequality in one or both, the values of N_1 and N_2 fluctuate and the greater the inequality, the greater the fluctuation. As the figures show, the general relation between the curves of N_1 and N_2 is similar in all the cases computed. A consequence of the theory adopted is that the paras te population does not reach its maximum when the host population is at its maximum but when the host population is halfway down to its minimum. The same feature occurs in the graphs of the Bailey-Nicholson equations. For this reason, G. C. Varley (1958), criticizing Nicholson's reasoning, considers that parasites and predators (assuming that they behave according to theory) should be called "delayed density-dependent factors". The point made by Varley is important. The mathematical models from which Nicholson reasons do not indicate that the action of the parasites and predators is most intense when the prey population is highest, nor least intense when it is lowest, though this is the characteristic of a controlling factor as defined by Nicholson.

It seems that there is a slight misunderstanding here. If, in the differential equation for N_2, which is:—

$$\frac{dN_2}{dt} = (-\epsilon_2 + \gamma_2 N_1)N_2$$

we make $N_1 = \frac{\epsilon_2}{\gamma_2}$ the value of $\frac{dN_2}{dt}$ becomes zero, which means that the population of the parasite is stable. If we increase it, the value of $\frac{dN_2}{dt}$ becomes positive, which means that at the instant considered, N_2 is rising; if we decrease the value of N_2, the value of $\frac{dN_2}{dt}$ becomes negative, which means that at the instant considered, the value for N_2 is falling. There is thus an instantaneous density-dependent response. What is delayed is not this response, but *the controlling effect*. This is evident also in the original mathematical model suggested by the present writer (1922) where the parasite population is increasing at the expense of an increasing host population, so that the reproductive capacity of the individual parasite is fully realized. Here also, the controlling effect is delayed. Parasites and predators of the type envisaged in these models can therefore be termed delayed controlling factors as compared with insecticides where there is, or may be, an instantaneous response to density which is an instantaneous increase in control measures.

As has been said, the formulae (4) (5) and (6) (7) for approximate integration, have been developed by neglecting certain terms. They apply to cases where the oscillations are small, that is, to cases where N_1 is not very far from $\frac{\epsilon_2}{\gamma_2}$ and N_2 not very far from $\frac{\epsilon_1}{\gamma_1}$. The greater the inequalities, the less the approximate curves will resemble those obtained by accurate integration ,e.g. with the Taylor theorem. Generally speaking in the cases computed with both integrations, the mean values of N_1 and N_2 are not very far from the theoretical values of $\frac{\epsilon_2}{\gamma_2}$ and $\frac{\epsilon_1}{\gamma_1}$. However, when the oscillations become very large, the equations (4) (5) give values far above the theoretical means. For example, if we put $N_1 = 100$, $\epsilon_1 = 0.5$, $N_2 = 20$, $\epsilon_2 = 0.4, \gamma_1 = \gamma_2 = 0.001$ in which case the relation $N_1: \frac{\epsilon_2}{\gamma_2} = 100:500$ and the relation $N_2: \frac{\epsilon_1}{\gamma_1} = 20:400$, the mean of N_1 is about 1500, as compared with the theoretical mean of 500. With the equations (6) (7) the mean of N_1 is 414, according to the writer's calculations. In the field of small oscillations, the amplitudes given by the two approximate equations are similar. For example, with $N_1 = 90$, $\epsilon_1 = 0.5$, $\gamma_1 = 0.01$, $N_2 = 50$, $\epsilon_2 = 0.4$, $\gamma_2 = 0.005$, the amplitudes with (4) (5) are $N_1 = 20$, $N_2 = 10$ and with (6) (7), $N_1 = 20$, $N_2 = 11$. Even with the ratios $N_1: \frac{\epsilon_2}{\gamma_2} = 100:66.6$, $N_2: \frac{\epsilon_1}{\gamma_1} = 40:50$, the amplitudes of N_1 and N_2 with equations (4) (5) are 69.5 and 44.5 as compared to 65.5 and 44.0 with the Taylor series of integration. However, with $N_1: \frac{\epsilon_2}{\epsilon_2} = 100:400$, $N_2: \frac{\epsilon_1}{\gamma_1} = 20:500$, the amplitude of N_1 given by equation (3) is about 8,300, but with the

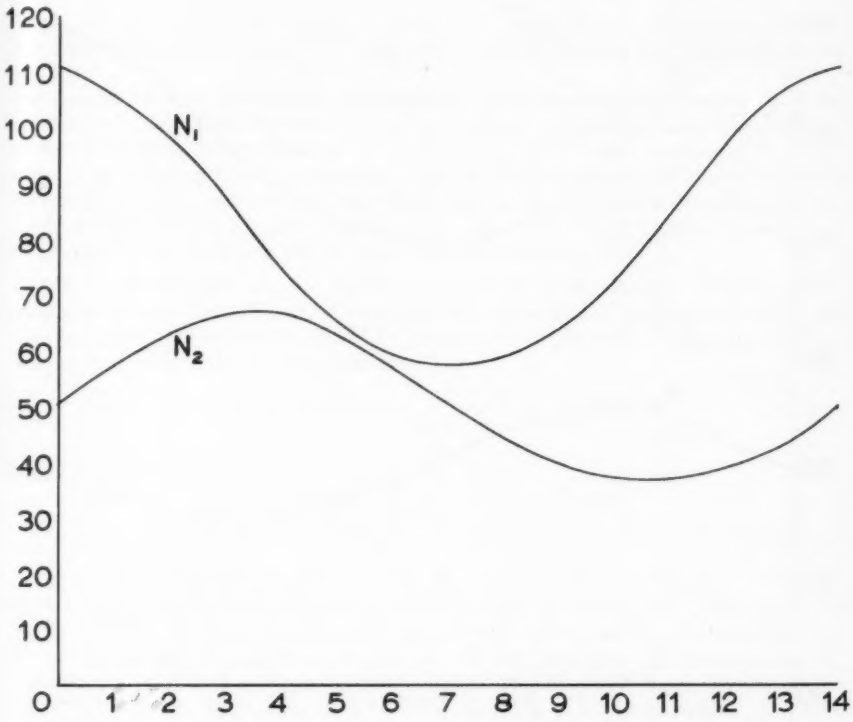

Fig. 5. $N_1 = 100$, $N_2 = 40$, $\epsilon_1 = 0.5$, $\epsilon_2 = 0.4$, $\gamma_1 = 0.01$, $\gamma_2 = 0.005$; integration with equations (4) and (5).

Taylor theorem, only 2,500. With $N_1 = 40$, $\epsilon_1 = 0.5$, $\gamma_1 = 0.001$, $N_2 = 100$, $\epsilon_2 = 0.4$ $\gamma_1 = 0.001$, the results with the three systems differ markedly. With (6) (7) the curve of N_1 is very flat, rising from a minimum of 100 to a maximum of about 700; with (4) (5) it rises steeply, from a minimum of about 25 to a maximum of over 5,000. With the Taylor series it is of intermediate form, extending from a minimum of 100 to a maximum of about 3,000.

Nevertheless, as the graphs show, the results with (4) (5) and the Taylor integration are quite similar for N_1: $\frac{\epsilon_2}{\gamma_2} = 100{:}66.6$, N_2: $\frac{\epsilon_1}{\gamma_1} = 40{:}50$, and do not differ enormously when we have N_1: $\frac{\epsilon_2}{\gamma_2} = 40{:}80$, N_2: $\frac{\epsilon_1}{\gamma_1} = 100{:}50$. The graphs for $N_1 = 100$, $\epsilon_1 = 0.5$, $\gamma_1 = 0.01$, $N_2 = 40$, $\epsilon_2 = 0.4$, $\gamma_1 = 0.005$, where we have N_1: $\frac{\epsilon_2}{\gamma_2} = 100{:}80$, N_2: $\frac{\epsilon_1}{\gamma_1} = 40{:}50$, and for $N_1 = 90$, $\epsilon_2 = 0.5$, $\gamma_1 = 0.01$, $N_2 = 50$, $\epsilon_2 = 0.7$, $\gamma_2 = 0.005$, are therefore presumably quite similar to those that would be given by the Taylor theorem. Generally speaking, the computations made suggest that while equations (6) (7) give accurate means over a rather wide range, equations (4) (5) give a better idea of the amplitudes and of the general form and relationship of the curves.

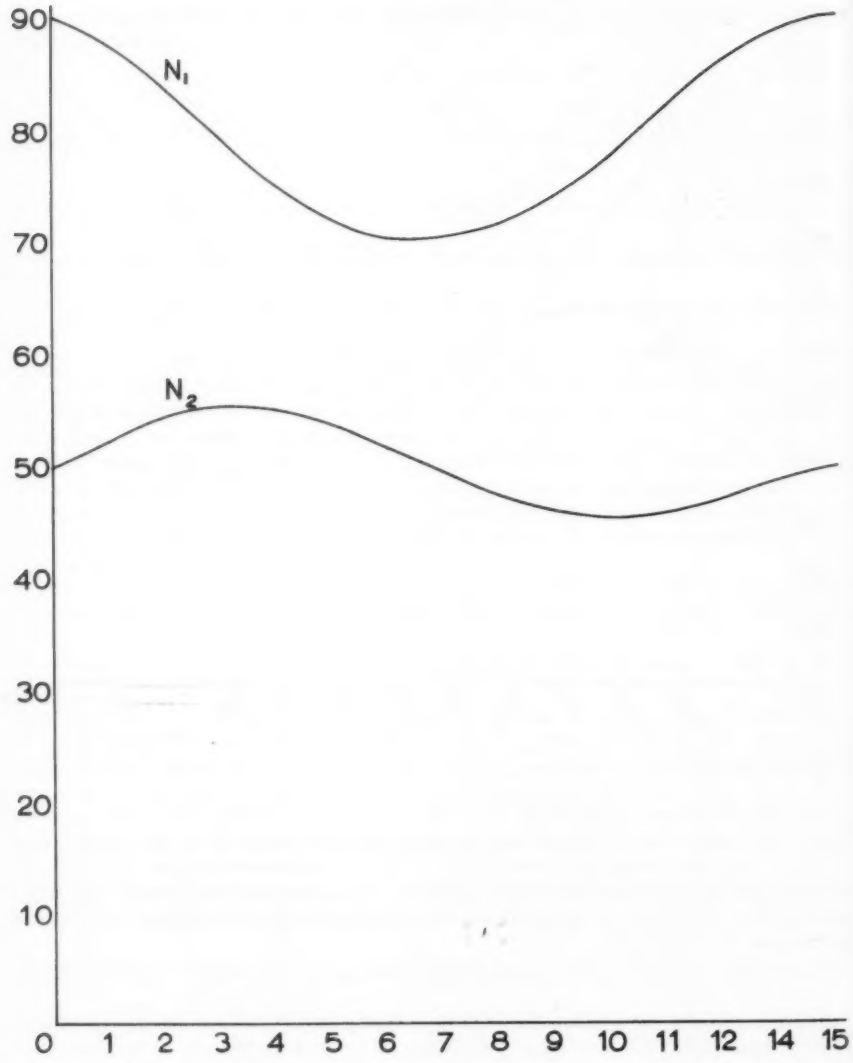

Fig. 6. $N_1 = 90$, $N_2 = 50$, $\epsilon_1 = 0.5$, $\epsilon_2 = 0.4$, $\gamma_1 = 0.01$, $\gamma_2 = 0.005$; integration with equations (4) and (5).

The fundamental reason for the difference is that the oscillations corresponding to (6) (7) are harmonic, the closed curves forming ellipses whereas the equations (4) (5) take into account the asymmetry implied in the original equations. This asymmetry is numerically shown by the fact that in the true curves for $N_1 = 40$, $N_2 = 100$, $\epsilon_1 = 0.5$, $\epsilon_2 = 0.4$, $\gamma_1 = 0.01$, $\gamma_2 = 0.005$, the interval from N_1 maximum to the mean $\left(\frac{\epsilon_2}{\gamma_2}\right)$ is 125, while the interval from N_1 minimum to the mean is 64; the interval from the

maximum of N_2 to the mean $\left(\frac{\epsilon_1}{\gamma_1}\right)$ being 103, while the interval from N_2 minimum to the mean is 35. The same curve calculated by the Volterra approximations gives the same interval (40) from the maximum of N_1 to the mean and from the minimum of N_1 to the mean; from the maximum of N_2 to the mean and from the minimum of N_2 to the mean (21). The same curves, integrated with (4) and (5), give an interval of 152 from N_1 maximum to the mean and an interval of 54 from N_1 minimum to the mean; and an interval of 80 from N_2 maximum to the mean with an interval of 32 from N_2 minimum to the mean. The characteristic asymmetry is thus maintained.

A comparison between the graphs gives an idea of the accuracy of the approximation in the examples selected. A more satisfactory method of judging the accuracy of the results was worked out by Dr. H. O. Hartley, of the Scientific Computing Service. The exact result, for N_1 (t), lies between:

$$\frac{\epsilon_2}{\gamma_2} e^{A \cos pt + \alpha} \quad \text{and} \quad \frac{\epsilon_2}{\gamma_2} e^{A \cos pt - \alpha}$$

where:

$$\alpha = \frac{A^2}{6}\left\{2.5 + \sqrt{\frac{\epsilon_2}{\epsilon_1}}\right\}$$

Thus, in an example where $N_1 = 100$, $N_2 = 40$, $\epsilon_1 = 0.5$, $\epsilon_2 = 0.4$, $\gamma_1 = 0.01$, $\gamma_2 = 0.006$, we get $\alpha = 0.14$ and therefore the exact value of N_1 (t) is between 1.15 N_1 (t) and 0.87 N_1 (t) as calculated by equation (4). For example, the maximum for N_1 will be between 125 and 95, approximately. In fact, it is 105. The minimum for N_1 will be between 46 and 35, approximately. In fact, it is 39. With $N_1 = 90$, $N_2 = 50$, $\epsilon_1 = 0.5$, $\epsilon_2 = 0.4$, $\gamma_1 = 0.01$, $\gamma_2 = 0.005$, we get $\alpha = 0.014$ so that $e^{+\alpha} = 1.014$ and $e^{-\alpha} = 0.996$ approximately. The maximum of N_1 will therefore be between 56.0 and 55.0 approximately. In fact, it is 55.25. The minimum of N_1 will therefore be between 45.8 and 45.0. In fact, it is 45.21. This illustrates the fact that in small oscillations the margin of error diminishes, while with large oscillations it increases.

The equations (4) (5) and (6) (7) are not, of course, mathematical models corresponding to the Lotka-Volterra hypothesis. They are rather mathematical strategems enabling us to get an idea of how this hypothesis works in concrete cases, when exact numerical values are substituted for the symbols, within the range where they can be safely used. On the other hand, these equations may be envisaged as purely mathematical hypotheses about the results of the interaction of prey and predator populations, to be tested by comparison of the numerical sequences obtained in laboratory experiments or field studies with those given by the formulae. The fact that the sequences derived from the formula do not lead to extinction like those derived from the Bailey-Nicholson formulae, is one point in favour of the Lotka-Volterra equations and of those giving similar results. The fact that the characteristic Nicholson-Bailey curves have been obtained in experimental studies does not constitute a verification with respect to events in nature. It rather suggests that there is something profoundly unnatural about the experimental situation because populations where prey and predator interact would long ago have disappeared if the basic theory were correct.

An interesting point about the "model" is that changes in the "initial values" of N_1 and N_2, such as might be produced by factors independent of density, such as weather, if followed by a stable condition might produce a very different type of fluctuation. This is exemplified in the Taylor graph of $N_1 = 40$, $N_2 = 100$, $\epsilon_1 = 0.5$, $\epsilon_2 = 0.4$, $\gamma_1 = 0.01$ $\gamma_2 = 0.005$, as compared with the one where $N_1 = 90$ and $N_2 = 50$, the other values remaining the same. In the first case there are violent fluctuations but with

the change in population values, these become scarcely noticeable, if plotted on the scale of the first graph.

Many other points of interest will certainly occur to those using the Volterra equations. This short paper does not pretend to exhaust the subject. It is mainly offered as a collection of handy recipes enabling ecologists to explore the basic hypothesis which sometimes presents serious difficulties to those with the usual modest mathematical equipment, but which still ranks as one of the classical contributions to population theory, developed by a most distinguished mathematician.

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(Received October 16, 1959)

Election of Officers of the Entomological Society of Canada

As a result of the recent balloting, the following members have been elected:

President-elect, 1960-61	A. W. A. Brown
Directors-at-large, 1960-62	D. A. Ross
	H. Hurtig
	N. P. Beaudoin
Directors representing regional entomological societies, 1960-62	C. J. S. Fox
	D. M. Davies
	C. R. F. Davis
	H. R. McCarthy
Honorary Member	J. B. Wallis

L. L. Reed,
Secretary.

Anatomical Characters Distinguishing *Bryobia arborea* M. & A. and *B. praetiosa* Koch (Acarina: Tetranychidae) from Various Areas of the World[1]

By C. V. G. MORGAN

Research Station, Research Branch, Canada Department of Agriculture
Summerland, British Columbia

On the basis of anatomical and ecological differences, Morgan and Anderson (1957) and Anderson and Morgan (1958) divided the *Bryobia praetiosa* complex of British Columbia into two species; the brown mite, *B. arborea* M. & A., 1957, found exclusively on fruit trees, and the clover mite, *B. praetiosa* Koch, 1836, found chiefly on herbaceous plants and known more commonly as a household pest. Acarologists in Switzerland, The Netherlands, and Russia have separated the complex into a number of species principally on anatomical bases (Pritchard and Keifer, 1958). In a recent exhaustive treatise of the complex in Switzerland, Mathys (1957) proposed five species and four 'forms'.

The splitting of the complex into species has not been readily accepted in North America. Pritchard and Keifer (1958) justifiably stated that it was difficult to evaluate the anatomical studies from a worldwide viewpoint because the work had been done solely on a local basis. Also, they considered that not all the anatomical distinctions presented were easy to appreciate. It is true that, lacking more definite anatomical evidence, most acarologists have relied largely on measurements of the length of the foreleg, or the length of the body, to separate the species.

This is a report on a comparison of specimens of *B. arborea* and *B. praetiosa* from North America, South America, Europe, Africa, and Australia. At least 4,000 mites were examined for the following anatomical features: the propodosomal anterior angulations, the propodosomal lobes, the dorsocentral hysterosomal setae, and the lengths of the foreleg and body.

Propodosomal Anterior Angulations

Several authors have included the structure of the propodosomal anterior angulations (Fig. 1) in drawings of the *B. praetiosa* complex, but none have mentioned the characters in the literature except in recent descriptions of species not of the *praetiosa* complex. The angulations are a pair of swellings on the fore margin of the propodosoma just proximad of the propodosomal lobes. Although the angulations do not bear setae, they may be considered as rudimentary propodosomal lobes. Ontogenetically the angulations develop much later than the lobes (Fig. 2). No indication of the site of development of the angulations is discernible in either the larva or the protonymph. Slight swellings are barely visible in the deutonymph, but the angulations are not identifiable until the mite reaches the adult stage. This characteristic development of the angulations can be used as a criterion for separating the immature stages from the adults of many *Bryobia* species.

The angulations are one of the best anatomical features for distinguishing the adults of *B. praetiosa* from those of *B. arborea.* They are always present in *praetiosa* but never in *arborea,* regardless of geographical occurrence or the plant host. The non-acarologist need not slide-mount the mites to observe the angulations; a good stereoscopic microscope adjusted for a magnification of 120 times, or more, readily reveals the swellings on *praetiosa.* Although slide-mounted

[1]Contribution No. 7, Research Station, Research Branch, Canada Department of Agriculture, Summerland, British Columbia.

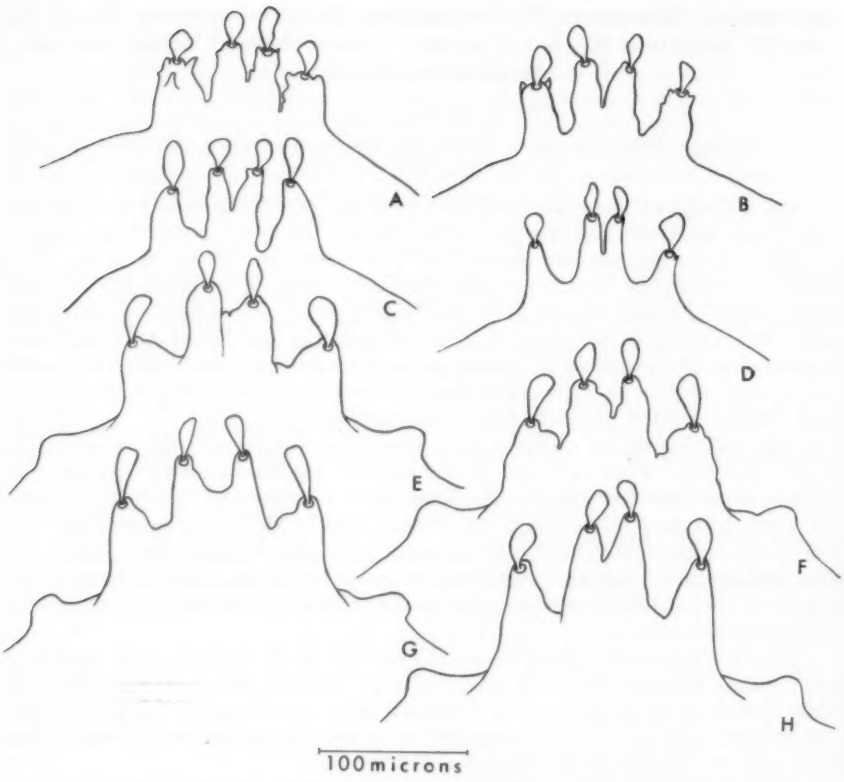

Fig. 1. Variations in shape of the propodosomal lobes and the propodosomal anterior angulations of adults of *B. arborea* (A-D) and *B. praetiosa* (E-H). Setal spines not shown.

specimens are preferred for detailed examination, clearing agents used before slide-mounting require careful manipulation as they may collapse or distort the angulations.

Propodosomal Lobes

The propodosomal lobes are two pairs of well-defined structures that project forward from the medial area of the anterior margin of the body. The lobes are a part of the dorsal integument and partially cover the gnathosoma. At its extremity, each lobe bears a seta that is somewhat similar in size and shape to the other dorsal setae. The lobes may be distinctly separated from each other, but more commonly they are fused for part of their length to form a distinct basal area. This fusion has progressed so far in some species, other than *arborea* and *praetiosa*, that the median pair of lobes appears as a pedestal tipped with two setae. The shape of the lobes is highly distinctive of many species; some are stubby, truncate projections, and others are graceful, fingerlike structures. Some individual mites develop only three lobes but that is an anatomical oddity.

Discrete, propodosomal projections first appear in the protonymph, but their final shape and size are not attained until the adult stage (Fig. 2). Where the shape of the lobes is a distinctive feature of the mite, this character may be

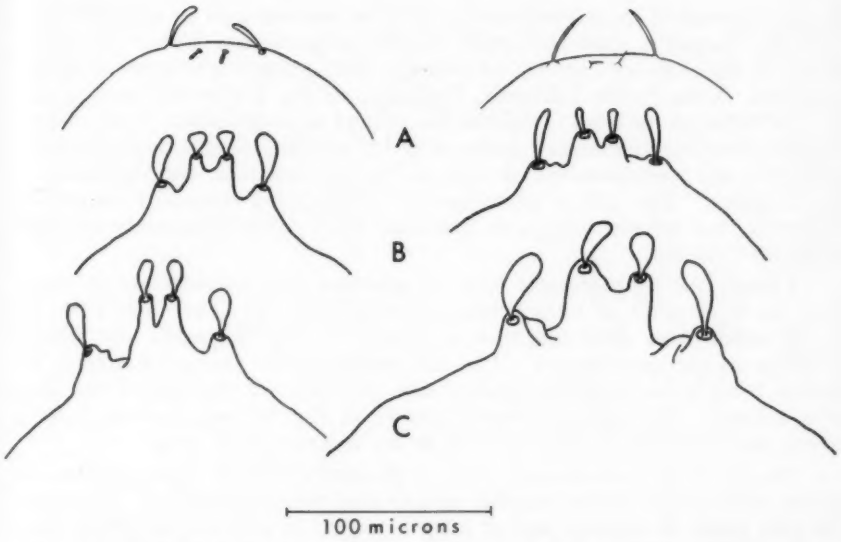

Fig. 2. Shapes of the propodosomal lobes in the larval (A), protonymphal (B), and deutonymphal (C) stages of *B. arborea* (left) and *B. praetiosa* (right). Setal spines not shown.

used to determine the species of protonymphs and deutonymphs. More often, however, the shape of the lobes may not be used taxonomically until the adult stage.

Although the propodosomal lobes are not present in the larval stage, two pairs of setae, similar to those that eventually adorn the lobes, occur at the site from which the lobes arise in the protonymph (Fig. 2,A). In the larval stage the median pair of setae are appreciably smaller than the lateral pair, and in some species they are often difficult to locate. They lie somewhat proximad of the anterior margin of the propodosoma, but in a transverse line with the lateral pair. The lateral pair are at the anterior margin of the propodosoma. In the adult stage the median pair lie anterad of the lateral pair. The position of the median setae in the larva apparently predetermines the dorso-ventral aspect of the propodosomal lobes in the adult. In the adult the median lobes lie slightly dorsad of the lateral pair even though there is some fusion of the basal areas of the lobes.

The propodosomal lobes have three characteristics that are useful in distinguishing adults of *B. arborea* and *B. praetiosa*: adventitious growths on the lobes, and shapes and sizes of the lobes. The adventitious growths have not been mentioned heretofore in the literature. They occur only on the lobes of *arborea* and may be small spines, thorns, or bud-like swellings (Fig. 1). Large variations occur in the size of the growths; some are minute and others, which are definitely spinelike in shape, are 12 microns or more long. Their numbers also vary considerably; some adults of *arborea* have lobes with as many as ten growths of various shapes whereas a very few have none. Although examples of all these variations can be found in practically every country, one or two may predominate in a specific locality. In Nova Scotia and The Netherlands the lobes and growths illustrated in Fig. 1,A, are common on *arborea* adults on apple. There

the development of the adventitious growths has reached such an advanced stage that they impart a grotesque shape to the propodosomal lobes. The lobes shown in Fig. 1,B, are common on *arborea* adults on pear and apple in British Columbia, Nova Scotia, California, England, and the Union of South Africa. In most countries the lobes of *arborea* mites found on peach, plum, prune, cherry, and pear bear few adventious growths (Fig. 1,C and D). Similar lobes, however, (Fig. 1,C) are not uncommon on apple in Turkey, Australia, and the Union of South Africa. Fig. 1,D, is an example of a type found frequently on pear in Argentina, but *arborea* mites with indentical lobes occur occasionally on apple in British Columbia.

Though the propodosomal lobes of *praetiosa* vary considerably in shape, they are a character of some taxonomic value (Fig. 1). The outer lobes are usually much wider at the base than in *arborea* and they frequently bear distinct swellings on the inner margin. The cleft separating the lateral lobes from the median lobes is comparatively shallow and never runs to the base of the lobes as in *arborea*. The lobes of *praetiosa* shown in Fig. 1,E and F, occur only in North America; those of Fig. 1,G and H, are common in all areas.

The size of the propodosomal lobes is of definite value in separating the two species; those of *arborea* are decidely smaller than those of *praetiosa*. In *arborea* the basal width of the two pairs of lobes averages 120 microns; the lateral lobes approximate 50 microns in length and the median ones about 65 microns. Respective measurements for *praetiosa* are 155, 65, and 100 microns.

Hysterosomal Setae

All adults of the *B. praetiosa* complex that were examined in this investigation bore only three pairs of dorsocentral hysterosomal setae. Some authors have illustrated four pairs in several species of the complex (Bagdasarian, 1957; Vitzthum, 1929). At least two species, *B. redikorzevi* Reck, 1947, and *B. osterloffi* Reck, 1947, though recently placed in synonomy with *B. praetiosa* (Pritchard and Keifer, 1958), bear four pairs as interpreted from the drawings of Bagdasarian (1957).

Unlike the adult, the *praetiosa* larva has on the hysterosoma four pairs of dorsocentral setae and one pair of sacral setae (Fig. 3, A and B). The fourth pair of dorsocentral setae are more widely separated than the third and lie decidely anterad of the posterior margin of the body. The bases of the sacrals, the clunals, and the fourth pair of dorsocentral setae form a triangular pattern on each side of the body. In the protonymph (Fig. 3,C) and all the later stages, the fourth pair of dorsocentral setae are in a marginal position between the clunals and the sacrals, and are called the inner sacral setae, the sacral setae of the larva being called the outer sacrals. In *arborea* the setal pattern of the hysterosoma of the larva (Fig. 3,D) is identical with that of the adult; there are only three pairs of dorsocentral setae, and the sacrals are always marginal in position. If we accept the theory of Pritchard and Baker (1955) that, in the higher forms of mites, the inner pair of sacral setae resemble a fourth pair of dorsocentral setae, whereas in the lower forms the sacral setae may be marginal, then the position of the hysterosomal setae on the larva of *praetiosa* suggests that this mite is somewhat more highly developed than *arborea*.

In 1957, Morgan and Anderson showed that, in British Columbia, the shape and position of the dorsocentral hysterosomal setae in the larvae are valid enough characters in themselves to separate *praetiosa* from *arborea*. Though larval specimens are scarce or non-existent in most collections, the few that were

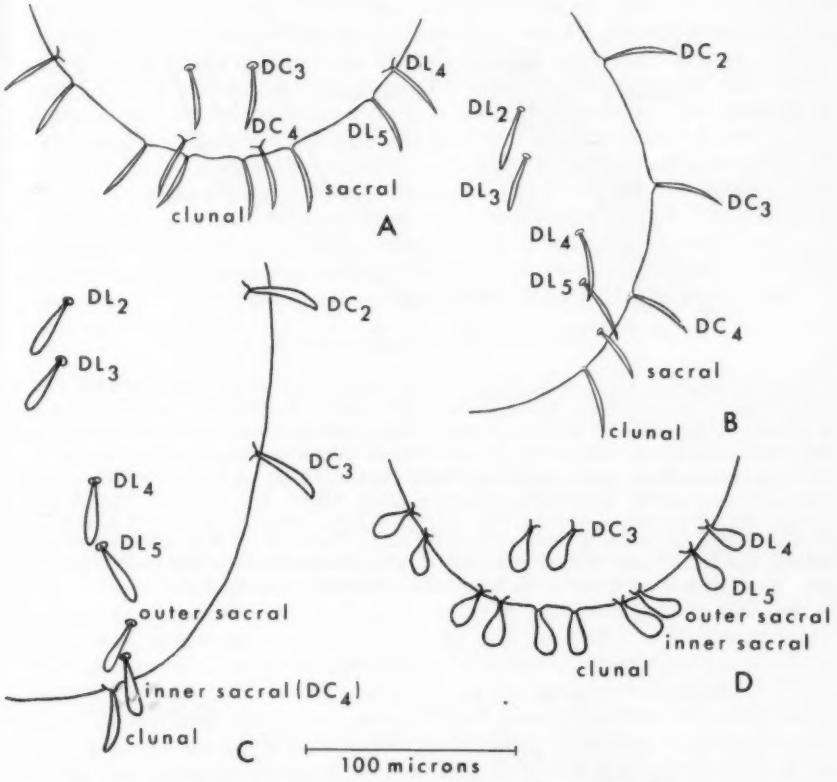

Fig. 3. Setal pattern of the posterior hysterosomal area of *B. praetiosa* and *B. arborea*. A, dorsal view of larva of *praetiosa;* B, lateral view of larva of *praetiosa;* C, lateral view of protonymph of *praetiosa;* D, dorsal view of larva of *arborea*. Setal spines not shown.

examined in this investigation bore setae similar in shape to those of British Columbia. In every case the larval setae of *arborea* were foliaceous like those of the adult, whereas those of *praetiosa* larvae were lanceolate and unlike the foliaceous setae of the adult (Fig. 3,A and D). Mathys (1957) used the shape of the larval setae as an aid in distinguishing five species and four forms in Switzerland, and, on the basis of this character alone, he subdivided the *Bryobia* mites of fruit trees into two forms that cannot be distinguished by any anatomical character in the adult stage.

The position of the dorsocentral hysterosomal setae is another excellent anatomical character that can be used to identify *arborea* and *praetiosa* irrespective of the country of origin, the host, or the stage of the mite (Figs. 4 and 5). In *arborea* the pattern of these setae is the same in all stages; DC_2 always lies mesad of an imaginary line joining DC_1 and DC_3 (Fig. 4). The setae of each pair lie fairly close together in the mid-dorsal region of the body. In the adult the setae of the DC_1 pair are separated by only about 65 to 80 microns, those of the DC_2 pair by 45 to 55 microns, and those of the DC_3 pair by 30 to 45 microns. The pattern formed by the same setae in *praetiosa* is almost the antithesis to that

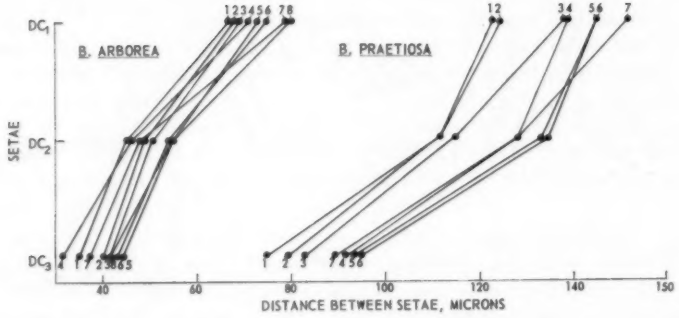

Fig. 4. Distances between the paired dorsocentral hysterosomal setae on adults of *B. arborea* and *B. praetiosa* from various areas of the world. Numbers of specimens measured as follows, in parentheses. *Arborea*: 1, apple trees, Adelaide, South Australia (2); 2, apple trees, California, U.S.A. (25); 3, peach trees, British Columbia, Canada (30); 4, apple trees, El Vergol, Chile (4); 5, apple trees, Nova Scotia, Canada (57); 6, apple trees, Wilhelminadorp, Holland (19); 7, apple trees, Elgin, Union of South Africa (10); 8, peach trees, Ontario, Canada (38). *Praetiosa*: 1, exterior walls of house, Nova Scotia, Canada (19); 2, grass near building, British Columbia, Canada (25); 3, in house, California, U.S.A. (16); 4, grass near building, Quebec, Canada (20); 5, grass near building, Saskatchewan, Canada (50); 6, exterior walls of house, Kent, England (13); 7, in house, Manitoba, Canada (25).

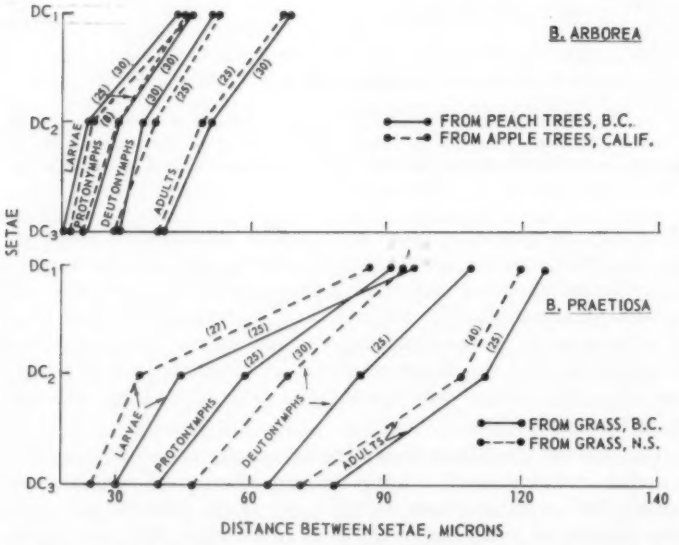

Fig. 5. Changes in distances between the dorsocentral hysterosomal setae during growth of *B. arborea* in British Columbia and California and of *B. praetiosa* in British Columbia and Nova Scotia. No data available for protonymphs of *B. praetiosa* from Nova Scotia. Number of specimens measured in each stage shown in parentheses.

found in *arborea* (Fig. 4). The setae are much farther apart in all stages of *praetiosa*, a distinguishing character in itself; however, the pattern formed by the bases of the larval setae, especially by DC_2 and DC_3, resembles that of *arborea* (Fig. 5). As the *praetiosa* mite grows through the protonymphal and deutonymphal stages, the DC_2 setae separate to a much greater extent than do those of the DC_1 to DC_3. As shown in Fig. 4 this pattern of the dorsocentral hysterosomal setae is distinctive of all *praetiosa* adults. Although the examples illustrated in this figure were collected from widely separated areas, there is remarkably little variation in the distances between these setae within each species. Nevertheless, the writer considers that, if the position of these dorsal setae is to be used as a character for separating other mites of the *praetiosa* complex, the pattern formed by the setae is a more reliable character than the distances between the setae.

Lengths of the Foreleg and Body

Until recent years the lengths of the foreleg and body were the principal characters used to separate *Bryobia* species. Although some workers denounced the characters because of supposedly overlapping variations, they were found to be valid for separating the adults of *arborea* and *praetiosa* in British Columbia (Morgan and Anderson, 1957). Also, the characters were used extensively for distinguishing the species in Switzerland (Mathys, 1957). Unfortunately, it is difficult to compare the results from various areas because workers in the various areas have used different criteria for measuring the lengths of the foreleg and the body. These different interpretations are, undoubtedly, partly responsible for the apparent variation in the two structures. In this investigation, and that of Morgan and Anderson (1957), the foreleg was measured from the proximal margin of the trochanter to the distal end of the tarsus, excluding the tarsal claws. The length of the body was measured from the posterior margin of the opisthosoma to the distal end of the propodosomal lobes, excluding the dorsal setae. Since the propodosomal lobes are not developed in the larva, the length of the body of that stage was obtained by measuring from the posterior margin of the opisthosoma to the anterior margin of the propodosoma.

On the basis of the above definitions it was shown in British Columbia (Morgan and Anderson, 1957) that the forelegs of the adults of *arborea* and *praetiosa* are always shorter than the body. The same relationship was found in all the samples examined in the present investigation except in a few samples of *arborea* from Australia and South America, where, in some individuals, the forelegs are longer than the body (Table I). Except for these mites, the ratio of the foreleg length to the body is approximately the same in the two species: in *arborea* it varies from 1:1.02 in British Columbia to 1:1.27 in England; in *praetiosa* from 1:1.04 in California to 1:1.18 in Quebec.

In British Columbia, an individual mite of *arborea* or *praetiosa* is identifiable by a measurement of either the foreleg length or the body length. In *arborea* the foreleg measures less than 690 microns and the body length is shorter than 740 microns; in *praetiosa* the adults have longer legs and longer bodies. The same characters may be used in most other areas except in Nova Scotia, Quebec, and California, where it is necessary to measure a number of mites. In Nova Scotia and Quebec, for example, the forelegs of some *praetiosa* adults are shorter than 690 microns. Also, in Nova Scotia and California, the body length of some *praetiosa* adults is less than 740 microns.

The characters of the foreleg length and the body length may also be used to separate the species in the immature stages (Table II). The forelegs are

TABLE I

Lengths, in microns, of the foreleg and body of slide-mounted adults of *B. arborea* and *B. praetiosa* from various areas of the world

Area	Host	Foreleg			Body		
		Number of specimens	Average	Range	Number of specimens	Average	Range
B. arborea							
British Columbia, Canada	Apple	56	522 ± 28*	413–575	74	531 ± 32	470–599
British Columbia, Canada	Peach	20	578 ± 21	543–608	20	617 ± 21	567–656
Nova Scotia, Canada	Apple	35	616 ± 27	568–681	57	654 ± 27	574–703
Calfornia, U.S.A.	Cherry	20	560 ± 56	494–616	23	620 ± 39	535–689
California, U.S.A.	Apple	17	535 ± 31	495–595	25	585 ± 31	516–645
California, U.S.A.	Almond	13	558 ± 20	527–583	15	639 ± 14	624–664
Kent, England	Plum	3	521	510–535	3	661	648–690
Wilhelminadorp, Holland	Apple	13	588 ± 37	551–664	20	665 ± 27	632–721
Elgin, Union of South Africa	Apple	8	574 ± 27	531–609	10	608 ± 33	559–653
Adelaide, Australia	Apple	2	599	566–631	2	584	574–595
El Vergol, Chile	Apple	3	588	566–617	4	538	466–609
Ankara, Turkey	Apple	—	—	—	4	563	523–609
B. praetiosa							
British Columbia, Canada	Grass	25	733 ± 37	725–873	25	826 ± 32	753–889
Saskatchewan, Canada	Grass	20	816 ± 62	713–915	23	879 ± 29	834–923
Manitoba, Canada	In house	25	808 ± 29	753–860	25	913 ± 44	860–1025
Quebec, Canada	Grass	29	746 ± 58	599–842	43	871 ± 48	745–956
Nova Scotia, Canada	House wall	12	709 ± 35	645–764	19	789 ± 49	703–853
California, U.S.A.	In house	16	799 ± 39	739–875	16	831 ± 57	731–939
Kent, England	House wall	10	786 ± 39	731–873	13	884 ± 32	839–939

*Standard deviation.

TABLE II

Lengths, in microns, of the foreleg and each of its segments and the lengths and the widths of the body, in microns, of the four active stages of *B. arborea* and *B. praetiosa* in British Columbia.

Character	Larva	Protonymph	Deutonymph	Adult
B. arborea				
Foreleg length	183 ± 7*	222 ± 8	316 ± 13	596 ± 18
Trachanter	20 ± 1	23 ± 2	27 ± 2	46 ± 2
Femur	51 ± 3	65 ± 3	104 ± 4	192 ± 8
Genu	31 ± 1	39 ± 1	52 ± 2	88 ± 2
Tibia	37 ± 2	46 ± 2	73 ± 3	160 ± 5
Tarsus	43 ± 3	49 ± 5	60 ± 6	110 ± 5
Body length	228 ± 19	333 ± 13	451 ± 14	623 ± 25
Body width	200 ± 10	260 ± 12	331 ± 10	430 ± 12
B. praetiosa				
Foreleg length	228 ± 11	296 ± 25	474 ± 23	773 ± 37
Trochanter	25 ± 2	30 ± 3	39 ± 3	59 ± 3
Femur	64 ± 4	92 ± 8	152 ± 7	251 ± 13
Genu	39 ± 2	52 ± 4	76 ± 3	119 ± 4
Tibia	47 ± 3	64 ± 7	114 ± 6	211 ± 12
Tarsus	53 ± 4	58 ± 6	93 ± 9	132 ± 10
Body length	303 ± 20	423 ± 32	645 ± 29	826 ± 32
Body width	242 ± 11	318 ± 31	465 ± 27	604 ± 29

*Average and standard deviation of 25 slide-mounted mites.

relatively much shorter than the body in the immature stages than in the adult. The growth rate of the two structures is approximately the same throughout the larval, protonymphal, and deutonymphal stages, but in the third quiescent stage, the foreleg elongates more than the body. Much of the growth of the foreleg occurs in the femur and the tibia, the two longest leg segments. Between the larval and adult stages the femur grows about 3.8 (*arborea*) to 3.9 (*praetiosa*) times and the tibia about 4.3 (*arborea*) to 4.5 (*praetiosa*) times, compared with 2.3 to 3.1 times for each of the other segments. Nevertheless, the tibia is shorter than the tarsus in the larval stage of both species. In *praetiosa*, the tibia grows much faster than the tarsus and exceeds it in length in the protonymphal stage. In *arborea* the tibia grows more slowly and does not surpass the tarsus in length until the deutonymphal stage. Like the tarsus, the other segments of the foreleg of *arborea* grow more slowly than those of *praetiosa* during the early nymphal stages. This trend is reversed between the deutonymphal and adult stages; the foreleg of *arborea* elongates about 1.9 times and that of *praetiosa* about 1.6 times.

Summary

B. arborea M. & A. is anatomically distinct from *B. praetiosa* Koch in North America, South America, Europe, Africa, and Australia.

An individual mite may be readily distinguished by the propodosomal anterior angulations in the adult (absent in *arborea*, present in *praetiosa*), the size of the propodosomal lobes in the adult (basal width about 120 microns in *arborea*, about 155 microns in *praetiosa*), the pattern of the dorsocentral hysterosomal setae in all stages (DC_2 lies mesad of a line joining DC_1 and DC_3 in *arborea* adults, laterad of this line in *praetiosa* adults), the shape of the dorsal setae in the larva (foliaceous in *arborea*, lanceolate in *praetiosa*), and the position of the sacral setae in the larva (inner pair marginal in *arborea*, resembling a fourth pair of dorsocentral hysterosomal setae in *praetiosa*).

The shapes of the propodosomal lobes, the presence or absence of spines or budlike swellings on the propodosomal lobes, and the lengths of the foreleg and

the body are also helpful diagnostic characters but, because they vary somewhat between countries, their use may be limited to local areas.

Acknowledgments

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(Received July 19, 1959)

A New Species of the Genus *Cinara* Curtis (Homoptera: Aphididae) from *Tsuga heterophylla* (Raf.) Sarg.[1]

By G. A. Bradley[2]

Aphids of the species described below were first seen by the author at Cowichan Lake, Vancouver Island, in 1956. Additional observations and collections were made in 1959 at several other locations in southern British Columbia.

The species is unique in that it is apparently the only one in the genus living on western hemlock, *Tsuga heterophylla* (Raf.) Sarg.

All measurements of the body and appendages are in millimetres.

Cinara tsugae, new species

Fundatrix

Colour of body dark brown, shading to amber brown on head and thorax. Eyes black. Antenna light brown, except tips of III, IV, and all of VI, which are dark brown. Cornicles and muscle attachment plates shiny black.

Measurements.—Nine specimens measured. Body, length, 3.16-3.38; width, 1.93-2.20. Width of head across eyes, .74-.77. Antenna, total length, 1.34-1.56; lengths of segments, III, .48-.58; IV, .17-.20; V, .23-.29; VI, base, .17-.21; unguis, .03-.04. Hind tibia, length, 2.33-2.63, width, .10-.12. Hind tarsal segments, I, .12-.15; II, .35-.36. Rostral segment IV, .17-.20. Rostrum extends to about the middle of the abdomen. Width of cornicle base, .17-.26. Length of setae, on antenna, .05-.06; on dorsum of abdomen, .02; on hind tibia, .05-.07. Number of sensoria on antennal segments, III, 0-1; IV, 0-1; V, 1-2.

Alate viviparous female

Colour of body shiny dark brown, without light powdery markings. The antenna is mainly dark in colour, except the basal third of III, which is light yellow. The femora of the pro- and mesothoracic legs in cleared specimens are light brown at their apices, shading to light yellow, nearly colourless at their bases; the femora of the metathoracic legs are dark brown on the apical two thirds, almost colourless near their bases. The tibia of the fore- and hind-legs is uniformly dark brown, except in some specimens in which there is an indistinctly lighter portion near the base. The tibia in the mesothoracic legs is dark brown just below the knee, light yellowish brown in the centre, and dark brown on about the apical third. The tarsi and coxae are all dark brown. The cornicle bases in cleared specimens are two shades of brown; the small raised, central portion of the cornicle is dark brown, while the surrounding sub-circular sclerotized area is light brown (Fig. 1, B). The medial vein of the fore-wing has two branches in both wings of five specimens, three branches in both wings of four examples, and in seven specimens it has two branches in one wing and three in the other.

Measurements.—Seventeen specimens measured. Body, length, 2.95-3.54; width, 1.34-1.56. Width of head across eyes, .65-.73. Antenna, total length, 1.28-1.54; lengths of segments, III, .50-.58; IV, .19-.23; V, .24-.29; VI, base, .11-.18; unguis, .04-.05. Hind tibia, length, 2.36-2.59; width, .06-.08. Hind tarsal segments, I, .12-.13; II, .31-.37. Rostral segment IV, .16-.18. Rostrum extends to about the middle of the abdomen. Width of cornicle base, .29-.35. Lengths of setae, on antenna, .04-.07; on dorsum of abdomen, .02-.03; on hind tibia, .05-.07. Number of sensoria on antennal segments, III, 5-8; IV, 1-2; V, 2. There are 11 basal setae on antennal VI.

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Apterous viviparous female

Abdomen chestnut-brown, head and thorax somewhat lighter brown. The pro- and mesothoracic legs in cleared specimens are almost entirely light brown, except the apices of the tibiae, and the tarsi, which are dark brown. The femora of the metathoracic legs are light brown at their bases, dark brown near the apices. The hind tibiae are light brown for about one-quarter of their length, following a very short dark brown portion just below the knees; the remainder of the tibiae, and the tarsi, are dark brown. Mesosternal tubercle but slightly developed. The muscle attachment plates are large and conspicuous (Fig. 1, A, m.a.p.).

Measurements.—Twenty specimens measured. Body, length, 2.95-3.54; width, 1.54-2.10. Width of head across eyes, .69-.77. Antenna, total length 1.28-1.52; lengths of segments, III, .48-.55; IV, .16-.25; V, .22-.29; VI, base, .15-.18; unguis, .04-.06. Hind tibia, length, 2.06-2.69; width, .09-.12. Lengths of hind tarsal segments, I, .12-.14; II, .32-.37. Length of rostral segment IV, .17-.20. Rostrum extends to the middle of the abdomen. Width of cornicle base, .20-.29. Lengths of setae, on antenna, .05-.07; on dorsum of abdomen, .01-.02; on hind tibia, .04-.06. Number of sensoria on antennal segments, III, 0-1; IV, 0-2; V, 1-2.

Oviparous female

Colour dull dark brown on the central portion of the abdomen, shading to a lighter brown on the thorax and head. A pericaudal wax ring is present, and consists of a thin, but distinct layer of white wax on the seventh and eighth abdominal segments. The cornicles are shiny dark brown. The bases of the cornicles are much smaller than they are in the viviparous females. Hind tibiae covered with numerous small, raised, circular sensoria.

Measurements.—Six specimens measured. Body, length, 2.61-2.92; width, 1.54-1.75. Width of head across eyes, .68-.70. Antenna, total length, 1.23-1.35; lengths of segments, III, .43-.47; IV, .15-.20; V, .24-.29; VI, base, .15-.16; unguis, .03-.04. Hind tibia, length, 1.82-2.05; width, .10-.11. Lengths of hind tarsal segments, I, .13-.15; II, .32-.37. Length of rostral segment IV, .16-.18. Rostrum extends to the middle of the abdomen. Width of cornicle base, .13-.17. Lengths of setae, on antenna, .05-.08; on dorsum of abdomen, .02; on hind tibia, .04-.07. Number of sensoria on antennal segments, III, 0-1; IV, 0; V, 1-2.

Egg

The egg is light yellowish brown in colour when first deposited, becoming jet black after a short time. The surface is covered with a thin layer of waxy powder. The egg is slightly kidney-shaped, and is attached to the needle along its concave surface.

Host

Tsuga heterophylla (Raf.) Sarg.

Life History

The eggs are laid on the needles near the ends of the branches, one egg to a needle, attached at about the middle of the lower surface of the needle. The fundatrices occur in groups of three or four on branches of about ¼″ to ½″ in diameter. They are found on young trees growing in the open, and also on suppressed trees in dense shade. The fundatrices and their nymphs later form dense colonies on the branches. Most of the aphids move down to the roots of the trees in early summer, the colonies being usually located near the root collar. In two instances the aphid colony was on the lower trunks of small, open-grown trees, as well as on the roots. In these locations the aphids were inside cone-

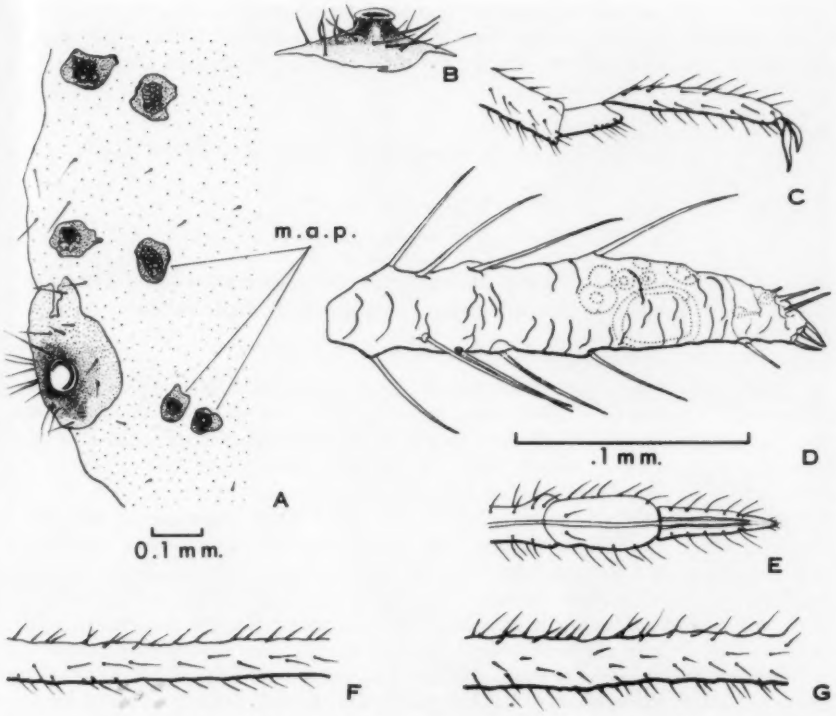

Fig. 1. *Cinara tsugae* Bradley n.sp. A, section of abdomen, apterous viviparous female, m.a.p., muscle attachment plates; B, cornicle, C, hind tarsus, D, sixth antennal segment, E, terminal segments of rostrum, F, section of hind tibia, alate female; G, hind tibia, apterous viviparous female. Scale of B, C, E, F, G, same as in A.

shaped shelters of soil particles erected around the trunks by ants, each shelter enclosing the trunk for about six inches above ground level. Numerous alate viviparous females are produced in the colonies on the roots and lower trunks by mid-July. These alates fly to other trees of the same species, where they begin feeding on the roots, and later deposit their nymphs in this location, forming new colonies. The aphids move up from the roots in the autumn, and the oviparous females deposit their eggs on the needles. Ants attended the aphid colonies throughout the season.

Type

Holotype, alate viviparous female, collected June 29, 1959, near Lumby, British Columbia, from *Tsuga heterophylla* (Raf.) Sarg. Morphotype, apterous viviparous female, collected July 30, 1959, at Christina Lake, B.C. Types and paratypes in the Canadian National Collection, Ottawa.

Distribution

Collected at Lake Cowichan, Vancouver Island; Lumby; and Christina Lake, British Columbia.

This species is somewhat similar to C. *pseudotaxifoliae* Palmer, from which it differs in the form of the cornicle bases, which are larger and more raised in

C. tsugae. The second segment of the hind tarsus and the fourth rostral segment are longer in *C. tsugae* than in *C. pseudotaxifoliae*. The setae on the dorsum of the abdomen are shorter, (.01-.03) in *C. tsugae* than they are in *C. pseudotaxifoliae*, (.06).

Main distinguishing characteristics

Short setae on dorsum of abdomen; large muscle attachment plates in the apterous females.

(Received December 16, 1959)

Notes on the Juniper Berry Mite, *Trisetacus quadrisetus* (Thomas) (Acarina: Eriophyidae), in British Columbia[1]

By C. V. G. Morgan[2] and A. F. Hedlin[3]

The juniper berry mite, *Trisetacus* (*Eriophyes*) *quadrisetus* (Thomas), was unknown in Canada until 1956, when its occurrence was noted on Rocky Mountain juniper, *Juniperus scopulorum* Sarg., in the Tzouhalem Indian Reserve near Duncan on Vancouver Island, B.C.; it has not been found elsewhere in the Province (Fig. 1). Material was first submitted to the authors by Mr. W. G. Ziller, Forest Biology Laboratory, Victoria, B.C. Each year almost the entire crop of berries on the only two trees in the area is destroyed by the mite; these trees are 30 and 50 feet high. In 1956 and 1957, no normal berries were observed. In 1959, only four healthy berries were found amongst 715 examined from the two trees. Such a heavy infestation indicates that seed production by these trees was practically eliminated since feeding by the mite destroys the seed.

The juniper berry mite was originally described from Europe on the common juniper, *Juniperus communis* L. (Hodgkiss, 1918; Keifer, 1957); it is well known in Poland (Kapuscinski, 1946; Borusiewicz and Kapuscinski, 1948). Though this eriophyid is a holarctic species it has seldom been reported in North America. In the United States it is known to occur only in New York and California. Leonard (1928) lists two varieties on juniper berries at Ithaca, N.Y.: *T. q. juniperinus* (Nal.) and *T. q. typicus* (Thomas). The mite in California, as in British Columbia, has been identified by Mr. H. H. Keifer, California State Department of Agriculture, Sacramento, Calif., only as *T. quadrisetus* (Thomas) (Keifer, 1952; Keifer, 1957). In California it destroys practically all the berries of many trees of the California juniper, *J. californica* Carr., and especially of the western, or Sierra, juniper, *J. occidentalis* Hook. (Keifer, personal communication). A related species, *Eriophyes ramosus* Hodgkiss, occurs near Williams, Arizona, where it deforms the fruit of the alligator juniper, *J. deppeana* Steud. (= *pachyphloea* Torr.) (Hodgkiss, 1918; Little, 1953). Essig (1958) calls this species the juniper mite.

A normal juniper berry is a smooth, round, green fruit containing one or two seeds but the number of seeds cannot be detected by the external shape of the berry. When infested with the juniper berry mite, the berry shrinks distally, wrinkles longitudinally, and turns a purplish colour. The number of seeds now is apparent; if the berry contained only one developing seed, a single shrunken knob is present. If it contained two seeds, a double knob is formed; mites are always present in both knobs (Fig. 2).

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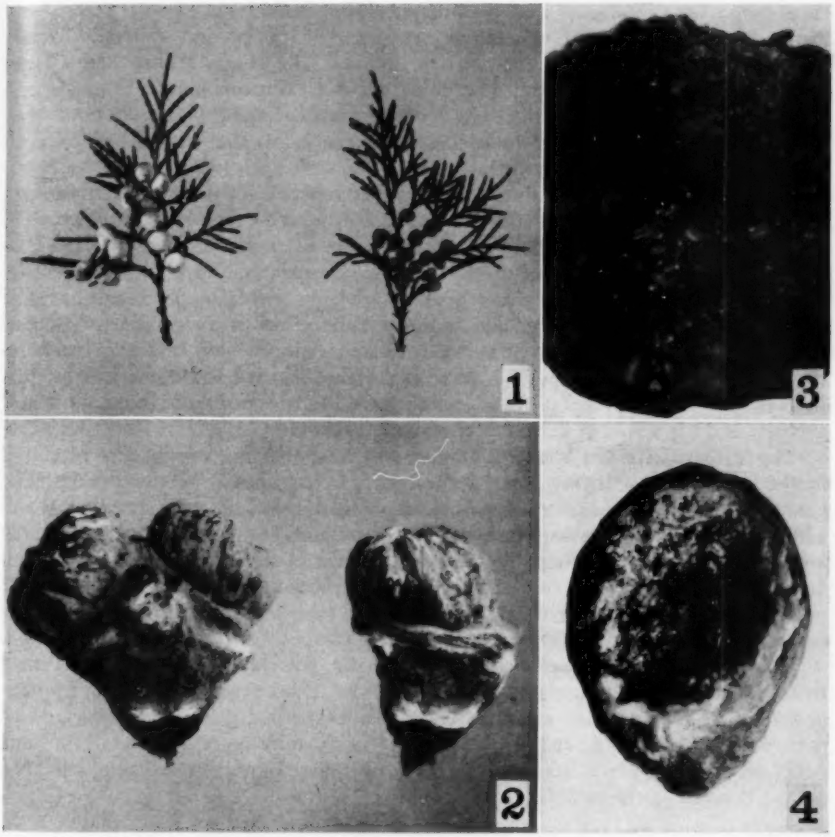

Figs. 1-4. The juniper berry mite, *Trisetacus quadrisetus* (Thomos). 1. Normal (left) and mite-infested (right) juniper berries. 2. Shape of the gall produced by the feeding of the juniper berry mite on double- and single-seed berries. 3. Interior view of gall showing eggs and other stages of the juniper berry mite. 4. Larva of *Tetrastichus* sp. near *silvaticus* feeding inside gall on the juniper berry mite. (Figs. 1, 2, and 4 by A. Craigmyle, Forest Biology Laboratory, Victoria, B.C.)

Characteristically, the basal part of an infested berry remains more or less normal and is distinctly separated from the knob by a waist. The end of the knob is dish shaped and bears a very small escape hole at its centre.

The knob is actually a gall-like structure containing hundreds of juniper berry mites in all stages of development (Fig. 3). Often, they are so numerous that the wriggling mass of mites appears to fill the entire cavity of the gall. The eggs, which can be found in the galls from early spring until late fall, are pearly white, translucent objects about 65μ long and 50μ wide. In 1957, they started to hatch in the latter part of May. The young mites are white in colour and more or less opaque but as they mature to the adult stage the colour changes to a light reddish brown.

The worm-like adult is a typical eriophyid. It ranges in length from 200 to 273μ and in width from 50 to 57μ. It is characterized by the presence of

three setae on the shield, one pair of subdorsal abdominal setae, the uniform distribution of abdominal microtubercles over the dorsal and ventral surfaces, and the absence of central lines on the shield. The single frontal seta of the shield is only about 12μ long. The dorsal setae are approximately 57μ long and are directed forward over the shield. These arise from tubercles placed well forward of the shield. The true claw just reaches to the end of the 8-rayed featherclaw.

The juniper berry mite lives almost exclusively within the juniper berry and is well protected from predators. However, it is severely attacked by two chalcid parasites, identified by Dr. O. Peck, Entomology Research Institute, Ottawa, as *Tetrastichus* sp. near *silvaticus* Gahan and *T. juniperi* (Cwfd.). Although true insect parasitism on mites is a rare phenomenon, the host-parasite relationship of gall forming eriophyids and chalcid parasites of the genus *Tetrastichus* has been known for many years, especially in Europe where *T. eriophyes* Taylor feeds on the currant gall mite, *Eriophyes ribis* Nal. (Zimmerman, 1913; Massee, 1928). In New York two species of *Tetrastichus* have been reared from juniper berries: *juniperi* and *marcovitchi* (Cwfd.) (Leonard, 1928).

In British Columbia both *T. juniperi* and *T.* sp. near *silvaticus* may be found in the same gall. Possibly one of these is a hyperparasite of the other. The chalcid larvae are present in infested berries throughout the summer and fall and adults emerge the following spring. Last-instar larvae of *T.* sp. near *silvaticus* are considerably larger than the mite host; they range in length from 1.31 to 1.92 mm. (Fig. 4). Of a total of 222 galls examined in 1956, 1957, and 1959, 72 per cent contained chalcid larvae. Despite this parasitism the juniper berry mite destroyed practically every berry each year.

No predators have been observed inside the galls; the escape hole is so small that predacious insects and mites cannot enter. The predacious mite, *Typhlodromus* (*Typhlodromus*) *arboreus* Chant, is frequently seen on the surface of galls where it probably feeds on the juniper berry mite when it moves from one berry to another. It is doubtful if this predation has any appreciable influence on the control of the eriophyid.

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Life-History and Behaviour of *Trogoderma parabile* Beal (Coleoptera : Dermestidae)[1]

By S. R. Loschiavo

Trogoderma parabile, a Nearctic species, was first described by Beal in 1954. In 1956 he reported it as a fairly common pest of granaries in California. In 1957, E. A. R. Liscombe (personal communication) recovered all stages of *T. parabile* in large numbers from flour mills and feed warehouses in Southern Alberta. In 1958, Brooks reported it from Saskatoon, Saskatchewan, where it occurred in several feed mills and was found infesting grain samples stored in small envelopes in the Science Service building. These reports are the first records of *T. parabile* in Canada. A closely-related Eurasian species, *Trogoderma granarium* Everts, is a serious pest of stored cereal products in hot dry parts of the world and is well-established in some parts of the United States and the United Kingdom but is not found in Canada. *T. parabile*, however, can adapt itself to colder conditions and may become a pest of economic importance in some parts of Canada.

The life-history of *T. granarium* is better known than that of any other species in the genus. Hinton (1945) reviewed the information on it up to 1945. Hadaway (1956) and Howe and Burges (1956) added to our knowledge of the taxonomy and biology of *T. granarium* and *Trogoderma versicolor* (Creutz.). In 1957, Burges worked on the identification and duration of the developmental stages of *T. granarium*. Except for a few known details of the biology, geographical distribution, and economic importance of *T. parabile* reported by Beal in 1954 and 1956 little is known about the species.

This paper deals with the duration of the life stages at 32° C. and 70 per cent relative humidity, the effect of disturbance on development, and the effect of low temperatures on survival and reproduction.

Methods

T. parabile was reared in the laboratory at 32° C. and 70 per cent relative humidity, these conditions being within the optimum range for several species of *Trogoderma*. One hundred and forty viable eggs 0-1 day old, selected at random, were reared individually in glass vials 60 mm. deep and 19 mm. in diameter each filled to about 30 mm. with a lightly-packed mixture of equal parts of finely-ground wheat and bran. Daily microscopic observations were made during development. Exuviae were removed after moulting and used to determine the number and duration of larval instars. The duration of each life stage was calculated as a range and arithmetic mean; the size, based on ten specimens was measured with a filar micrometer, within one day of emergence and descriptions of color, shape, and habits were noted.

Individuals were handled and examined for brief periods at temperatures and humidities lower than those of the experiment. As daily disturbance of this nature might retard development, one group of newly-emerged larvae was handled in the same manner as the life-history group, another was exposed for brief daily periods in the laboratory where the temperature fluctuated between 21° and 28° C., and a third was left undisturbed during the first 33 days of development when semi-weekly examinations were started. Percentage development and duration of the developmental period were determined for the three groups. Another experiment was similarly conducted to determine the percentage development of disturbed and undisturbed insects reared at 32° and 35° C.

[1]Contribution No. 34, Canada Department of Agriculture Research Station, Winnipeg, Manitoba.

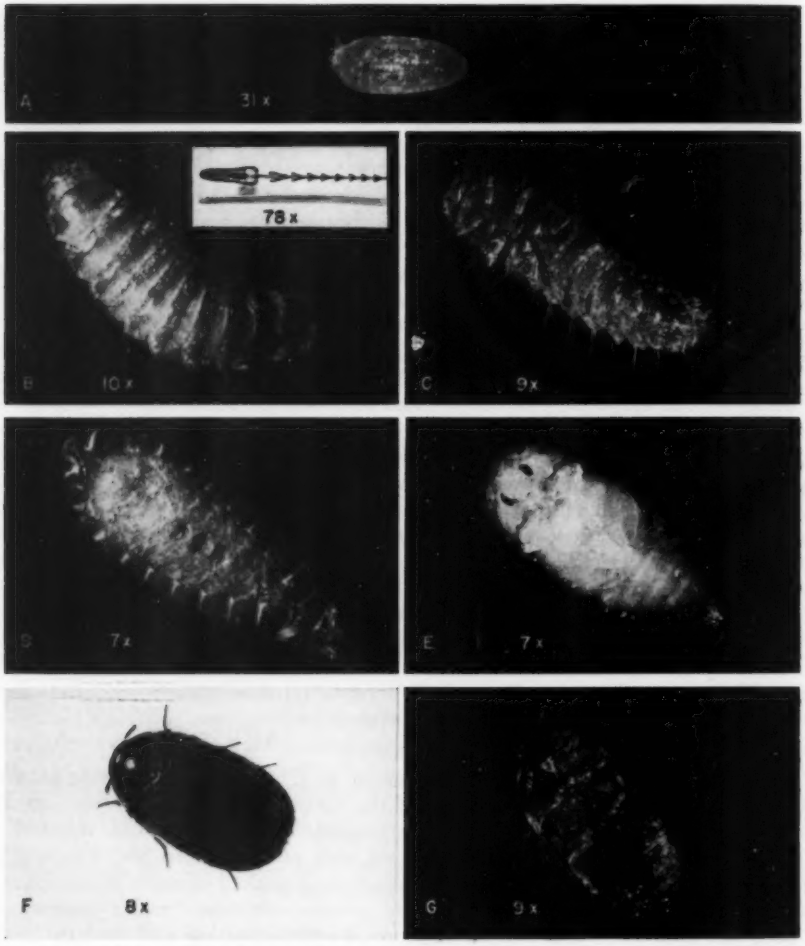

Fig. 1. Life stages of *T. parabile;* A. egg; B. and C. mature larvae, dorsal and ventral view respectively (inset shows simple and barbed hairs); D. pupa in last larval skin, dorsal view; E. pupa removed from last larval skin, ventral view; F. and G. adults, dorsal and ventral view respectively.

Adults four days old held at 70 per cent relative humidity in desiccators were exposed at 10°, 20°, and 32° C. for seven days to determine the effect of low temperatures on mortality and reproductive ability. Mature larvae held at the same conditions were exposed at −1°, 10°, and 20° C. for six days and their mortalities were assessed.

Results and Discussion

Life-history

Eggs were deposited singly in glass vials, salve tins, on blotting paper, loosely in crushed wheat, or in the crevices on whole kernels. During oviposition the ovipositor was protruded posteriorly. The newly-laid egg is pearly-white, translucent, extremely fragile, and covered with a sticky secretion. After two

TABLE I

Dimensions of developmental stages (based on 10 individuals)

Stage	Length of body (mm.)			Width (mm.)		
	Range	Mean	Standard error	Range	Mean	Standard error
Egg	0.54–0.71	0.63	±0.01	0.23–0.30	0.26	±0.00
First instar larva	0.84–1.04	0.92	±0.02	0.18–0.22	0.21[1]	±0.00
Second instar larva	1.38–1.68	1.56	±0.03	0.25–0.27	0.26[1]	±0.00
Third instar larva	1.45–1.62	1.54	±0.01	0.34–0.37	0.36[1]	±0.01
Fourth instar larva	2.64–3.15	2.90	±0.05	0.50–0.54	0.52[1]	±0.01
Fifth instar larva	3.68–4.65	4.17	±0.08	0.64–0.66	0.64[1]	±0.00
Sixth instar larva	4.63–5.15	4.89	±0.15	0.71–0.78	0.75[1]	±0.01
Pupa ♂	4.31–4.62	4.42	±0.07	1.53–1.80	1.71	±0.06
Pupa ♀	6.24–6.69	6.43	±0.10	2.42–2.69	2.54	±0.05
Adult ♂	2.77–3.06	2.93	±0.02	1.48–1.84	1.70	±0.03
Adult ♀	3.26–4.20	3.68	±0.09	1.90–2.35	2.08	±0.05

[1]Width of head.

or three days it is less fragile and can be handled safely with a soft-haired brush. When inspected microscopically the chorion appeared sculptured like a peanut shell. A typical egg (Fig. 1A) is cylindrically elongate and bears a number of hairs at one end; a few eggs are banana-shaped. Table I shows the dimensions and Table II the duration of the egg stage. The mean ratio of length to width was 1.0:0.4. Five per cent of the eggs failed to hatch. The developing larva was clearly visible through the transparent egg membrane about a day before hatching and gave the egg a reddish-brown appearance. Five distinct brown spots or ocelli were visible on each side at the anterior end of the egg. The posterior end was dark brown owing to the coiled, long, simple hairs of the last abdominal segment. The segments and erectile hairs on the dorsal surface were clearly visible in the developing larva. Shortly before hatching bulging movements occurred at different locations on the surface of the egg.

The egg ruptures at the anterior end. The first-instar larva emerges head first gradually pushing itself from the egg case with its legs and stopping periodically to rest. As the larva emerges the long brush-like "tail" slowly unwinds. After emergence the larva crawls about actively in search of food. The larva (Fig. 1, B, C) has, on the last abdominal segment, a number of long simple hairs directed posteriorly to form a long "tail" increasing in length with each succeeding instar. The mean length of the "tail" in the first-, second-, third-, fourth-, fifth-, and sixth-instar larva was 1.6, 0.9, 0.6, 0.5, and 0.4 times the mean body length respectively. Although the ratio of tail length to body length decreased with each successive instar the variation in this ratio between and within instars was too large to make tail length a useful criterion of instars. Simple hairs projecting laterally and dorsally occur over the entire surface of the body; barbed hairs (Fig. 1B, inset) occur in paired tufts on the body segments and in

TABLE II

Duration of developmental stages at 32° C. and 70 per cent relative humidity

Stage	Number of days			
	Number of insects	Range	Mean	Standard error
Egg	133	6–8	6.9	—
First instar larva	117	4–6	5.2	—
Second instar larva	112	3–6	4.7	—
Third instar larva	111	3–7	4.9	—
Fourth instar larva	109	4–7	5.4	—
Fifth instar larva	106	3–10	6.4	—
Sixth instar larva	102	3–10	7.4	—
Pupa	13	2–6	4.1	—
Adult life span	13	8–20	14.3	±1.16
Larva total	102	28–40	34.0	±0.25
Egg laid to adult emergence	13	39–50	43.2	±1.13
Egg laid to adult emergence from larval skin	13	41–55	45.9	±1.42

fourth, fifth, and sixth instars are particularly dense on the fifth, sixth, seventh, and eighth abdominal tergites. These features also occur in *T. granarium* and *T. versicolor* (Hadaway, 1956). The head bears three-segmented antennae with simple setae occurring on the mesal side of the basal segment only (Beal, 1954). Six ocelli are present on each side of the head, five forming a crescent-like configuration. The prothorax is the longest of the body segments. The first-instar larva is yellowish-white but later instars are reddish-brown and usually dark brown just before moulting. During moulting the skin splits along the mid-dorsal line fom the head to about the sixth abdominal segment and the larva crawls out leaving the cast skin behind. Larvae are active feeders and have strong mouth parts capable of chewing holes through acrylic plastic 1.7 mm. thick. From the first- to the fourth-instar, larvae cast their skins on the surface of the food and penetrated not more than four millimeters into it; subsequent instars tunnelled through the food and cast one out of three skins beneath the surface.

Table I shows the dimensions and Table II the duration of each larval instar. Head width was a less variable dimension than body length and therefore a more reliable means of differentiation between instars. The greatest increase in size occurred between the third and fourth instars. The duration of each larval instar was progressively longer. The larval period was normally completed in six instars but many fully-developed larvae moulted 28 times in 11 months and did not become pupae (see section on effects of disturbance on development).

The pupal stage is passed in the last larval skin. At the last moult the larval skin splits dorsally but is not cast off. The pupa, being wider than the larva, forces the skin apart leaving the dorsal surface visible through the gap (Fig. 1D). It has a thin transparent skin which, at adult emergence, is passed to the

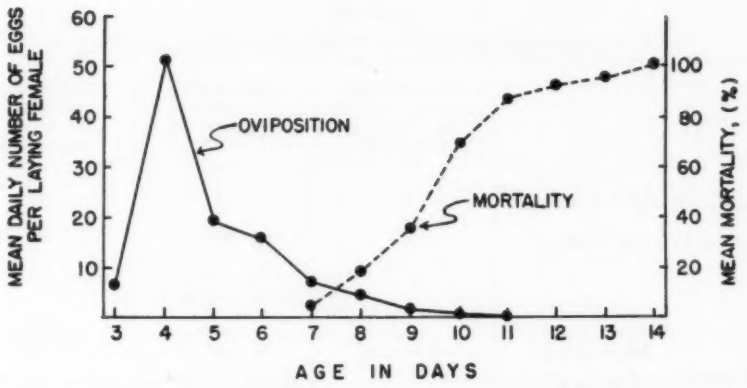

Fig. 2. Mean daily rate of oviposition and per cent mortality of 22 mated females.

posterior end of the larval skin. Fig. 1E shows a ventral view of a pupa removed from the larval skin. More than 90 per cent of the pupae are found at or near the surface of the food. Table I gives the dimensions of male and female pupae and Table II the duration of the pupal stage. Males are distinctly smaller than females.

The newly-emerged adult spends from one to seven days within the larval skin the average being about two days. It is a small, oval, black beetle covered with a fine pubescence. The elytra have distinct reddish-brown maculae which vary considerably in pattern within the species. The head is very small in relation to the rest of the body and is almost entirely covered by the pronotum. Fig. 1F, G show the adult in dorsal and ventral aspect respectively. Table I shows that the male is smaller than the female. The ratio of width to length is 1:1.8 in females and 1:1.7 in males. The adult lives from eight to 20 days, the mean life span being 14.3 days. Table II shows the duration of the life cycle and the mean time from oviposition to emergence of the adult from the larval skin.

Copulation occurs shortly after emergence. A few females laid eggs shortly after copulation but most of them did not commence laying until after a pre-oviposition period of one to two days. Some mated females laid as many as 65 eggs in one day; others fed on a medium consisting of ground wheat, bran, wheat germ, and brewer's yeast in the ratio of 45:45:5:5 laid as many as 94 eggs in one day. In this experiment virgin females were not observed to lay eggs. Fig. 2 shows that maximum oviposition occurred among females three to five days old. Females older than seven days laid few eggs and lived only a few days after oviposition ceased. Mortality increased from about 5 to 100 per cent from the seventh to the fourteenth day.

Females given a choice of oviposition sites between scored and unscored surfaces of blotting paper laid 95 per cent of their eggs in the loose fibers on the scored surface. Adults normally crawl but if handled roughly or upon reaching the edge of a plane surface they will spread their wings and fly in an almost vertical ascent.

Effects of Disturbance on Development and Diapause

Table III shows that the duration of the developmental periods in disturbed and undisturbed individuals was similar but that fewer individuals entered the adult stage in disturbed than undisturbed groups. In all groups, little adult

TABLE III

Effect of disturbance on development[1]

	Handled and exposed daily to room temperature (21° to 28° C.)	Exposed daily to room temperature (21° to 28° C.)	Undisturbed during first 33 days of development
Number of adults to emerge	11	21	38
Number in larval diapause	45	35	18
	Number of days from egg to adult (emergence from larval skin)		
Range	41–54	39–59	36–63
Mean ± S.E.	46.4±1.05	46.5±1.16	44.7±0.79
Mean ± S.E. based on number emerging in 48 days	45.2±0.79	44.2±0.79	43.5±0.52

[1]56 eggs 0–12 hr. old reared individually, at each condition.

emergence occurred after 48 days. Twenty and 68 per cent of disturbed and undisturbed insects respectively completed development; 80 and 32 per cent respectively entered larval diapause; 37 per cent of partially disturbed insects (i.e., those exposed for brief periods daily to fluctuating laboratory temperatures) completed development, and 67 per cent entered larval diapause. The term diapause is used here in the same sense as used by Burges (private communication, Pest Infestation Laboratory, Slough, Bucks, England). He has applied the term to mean an arrested development which persists in favorable conditions for a long time despite the correction of any factor suspected of delaying development. He states: "non-diapausing larvae complete their development in a short time, but in the same conditions the development of diapausing larvae appears to stop at the full grown larval stage although moulting continues". In another experiment 15 and 19 per cent of disturbed insects and 58 and 46 per cent of undisturbed insects completed development at 32° and 35° C. respectively.

Larvae that failed to develop into pupae or adults entered diapause after the sixth larval instar. At this stage larval development was complete but larvae continued to moult at irregular periods. Generally, in the life-history group, as larvae grew older the period between moults became longer, the longest being 40 days. In 11 months diapausing larvae had moulted 15 to 28 times, the mean being 19.7, and in 19 months had not entered the pupal stage. No larva in diapause has been observed to pupate. The longest observed period between moults in diapausing larvae was 63 days. The data on the effects of disturbance indicate that daily disturbance and handling is an important factor in diapause. However, 32 per cent of relatively undisturbed insects entered larval diapause. Burges (private communication) found that the amount of space was an important factor affecting the incidence of diapause. His data showed that about 65 to 88 per cent of larvae kept singly in 15 ml. of food or less entered diapause but only two to eight per cent of those with adequate food did so even in crowded cultures.

Effect of Low Temperatures

Table IV shows that young adults exposed seven days at 10° C. suffered no mortality but laid no eggs. Adults at 20° C. laid fewer eggs than those at 32° C.

TABLE IV

Mortality and reproduction of adults, four days old, exposed for seven days at 10°, 20°, and 32° C.

Temp. (°C.)	No. of pairs	Percentage mortality		Total no. of eggs	No. of laying females	Mean no. of eggs per laying females	Percentage hatch
		♂	♀				
10°	20	0	0	0	0	—	—
20°	25	12	4	399	14	28.5	0
32°	45	38	53	1107	29	38.2	98

and none of these hatched (Table IV). The eggs were misshapen and clustered together suggesting that these exposures may effectively prevent propagation. At 32° C. mean adult mortality was 45 per cent; female mortality was higher than that of males. The percentage of actively laying females was 64 at 32° C. and 56 at 20° C. Most of the eggs laid at 32° C. hatched. Mean daily egg production per female at 20° and 32° C. was not determined because of the variability in rate of oviposition, some females laying no eggs in seven days. At low temperatures adult survival was high but no progeny were produced. At higher temperatures low adult survival was associated with a high production of progeny.

Table V shows that a five-day exposure at 10° C. prevented oviposition but had no effect on the survival of newly emerged, mated females. During an exposure period of a further five days at 32° C. these females laid their maximum number of eggs. A second group of females exposed at 32° C. for both five-day periods laid most of their eggs during the first five days. This result is in agreement with the data shown in Fig. 2. Short exposures at low temperatures evidently inhibit oviposition but only temporarily. Higher mortality, particularly among females, occurred when insects were kept at 32° C. than when exposed first at 10° C. and then at 32° C. Perhaps exposure at a low temperature slows the rate of metabolism and thereby increases adult longevity.

Mature larvae reared at a constant humidity of 70 per cent were not killed during or after a six-day exposure at −1°, 10°, and 20° C. The presence of all life stages in an unused flour mill and warehouse that had been unheated the previous winter shows that *T. parabile* can survive winter temperatures in some

TABLE V

Mortality and reproduction of 20 pairs of adults, 0-1 day old, exposed at 10° and 32° C., and 20 pairs at 32° C.

Periods exposed (days)	Temp. (°C.)	Percentage mortality		Total no. of eggs	No. of laying females	Mean no. of eggs per laying female	Percentage hatch
		♂	♀				
0–5	10°	0	0	0	0	0	—
6–10	32°	5	15	502	12	41.8	84
0–5	32°	10	30	415	9	46.1	96
6–10	32°	30	30	69	7	9.8	93

parts of Canada. Therefore exposure at low temperatures is not, in itself, an effective control measure. At optimum temperatures it can reproduce and increase rapidly. Its ability to adapt itself to a wide range of temperatures and its high reproductive ability makes *T. parabile* a potentially serious pest of stored cereals.

Summary

In the laboratory at 32° C. and 70 per cent relative humidity the egg stage of *Trogoderma parabile* Beal lasted 6.9 days, each of six larval instars 5.2 to 7.4 days and the pupal stage 4.1 days. The duration of each larval instar increased progressively from the second to the sixth, the total larval period lasting 34 days. The mean adult life span was 14.3 days and the mean life cycle 43.2 days. Each life stage was measured and described. The greatest increase in size occurred between the third and fourth larval instars. Female pupae and adults were larger than their male counterparts.

Single, mated females laid from 0 to 94 eggs in one day, 95 per cent being hatchable. A short pre-oviposition period preceded a period of maximum egg production occurring in females three to five days old. Females older than seven days laid few eggs and lived only a few days after oviposition ceased. Rate of mortality increased rapidly in females older than nine days.

Daily disturbance of insects during development inhibited adult emergence but had no appreciable effect on rate of development. A high percentage of disturbed insects entered larval diapause.

A one-week exposure at 10° C. prevented oviposition but did not affect the survival of young mated females. At 20° C. many eggs were laid none of which hatched. At 32° C. high egg production was associated with high adult mortality, particularly among females. Although oviposition of young mated females was inhibited during a five-day exposure at 10° C. maximum oviposition took place when the temperature was increased to 32° C. Mature larvae were not killed by a six-day exposure at 20°, 10°, or —1° C.

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(Received November 20, 1959)

Relationship between Grasshopper Abundance and Weather Conditions in Saskatchewan, 1930-1958[1]

By Roy L. Edwards

The statement of Criddle (1917) that grasshopper outbreaks are associated with periods of dry weather has been repeated by many authors, but a close relationship has never been demonstrated.

Parker (1933) showed that at six localities in the United States grasshopper outbreaks during the period 1915-1933 had been preceded by periods of two to four years when either rainfall had been below normal during May-June or temperature had been above normal during July-September. Similarly Smith (1954) concluded that between 1910 and 1953 outbreaks in Kansas had been preceded by two years of sub-normal rainfall. Parker's charts show that grasshopper outbreaks generally followed periods of hot weather, but the charts of both authors show that only about half the time did outbreaks follow periods of dry weather – a situation that could be largely due to chance.

MacCarthy (1956) calculated the correlation coefficients between weather factors and populations of *M. bilituratus* (Walker) in five large areas of Saskatchewan during the period 1943-1952. His tables show generally insignificant correlation with total precipitation and only with mean minimum monthly temperature in June of the previous year was there significant correlation in all five areas.

The present investigation was undertaken in an attempt to determine whether a sufficiently close relationship between grasshopper populations and climate could be found for use in predicting grasshopper outbreaks.

Materials and Methods

From the Monthly Record of Meteorological Observations in Canada (1930-1956) and the Monthly Weather Map (1957-1958) data were obtained for 19 weather stations in that part of Saskatchewan where grasshopper outbreaks have often occurred. These data were compared with the mean density of the grasshopper population, expressed as numbers per square yard, in the Rural Municipality where the weather station was situated – or the two adjacent Rural Municipalities if it lay near the boundary between them. Each study area was therefore between 300 and 600 square miles in extent with the majority being nearer 300 square miles (Fig. 1).

The mean density of grasshoppers was obtained from survey sheets which have been compiled annually since 1932 by the staff of the Entomology Laboratory at Saskatoon. During August observers stop every five to six miles along routes 12 to 20 miles apart and estimate the density of the grasshopper populations both in the field and on the roadside. Although the ratio between these two populations varies greatly, their fluctuations approximately coincide, and this study has therefore been confined to the field population only.

Since 1943 separate estimates have been made of the four economic species *Melanoplus bilituratus* (Walker), *M. bivittatus* (Say), *M. packardii* Scudder and *Camnula pellucida* (Scudder). As the survey sheets showed that the species tend to fluctuate in unison no attempt has been made to treat them separately.

From the raw data outliers were eliminated at the one per cent level of confidence using Grubbs (1950) test for outlying observations. In years when grasshoppers were scarce the observers made fewer stops and there were only five to ten estimates for each study area. However, the estimates were consistent

[1]Contribution No. 44, Canada Department of Agriculture, Research Station, Saskatoon, Saskatchewan. Part of this paper was read at the meeting of the Royal Society of Canada at Saskatoon in June 1959.

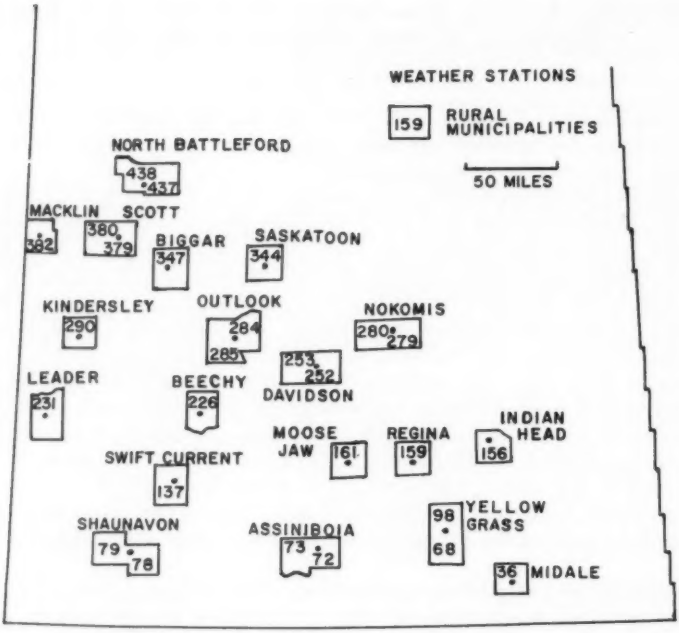

Fig 1. Map of southern portion of Saskatchewan showing the distribution of the weather stations and the numbers of the Rural Municipalities used in the study.

and their standard error was about five per cent of the mean. When grasshoppers became abundant observers made more stops and there were more estimates on which to calculate the mean, but owing to the patchy distribution of the grasshopper populations they showed considerable variation. It was therefore arbitrarily decided to reject all estimates whose standard error exceeded 40 per cent of the mean.

As preliminary tests showed that the mean of the population estimates bore a linear relationship to both temperature and precipatation the product-moment method of correlation was used.

Results

Temperature

The detailed investigation was confined to a consideration of the mean monthly temperature, as preliminary investigations showed this gave a generally higher correlation than the highest monthly temperature, lowest monthly temperature, mean maximum temperature or mean minimum temperature.

Correlation coefficients were calculated between grasshopper density and the mean monthly temperature for 66 different periods between May and October during the same and up to five preceding years. Of these, the highest correlations – which were all positive – were obtained with the total mean monthly temperature during: (1) July of the previous three years, (2) June-September of the previous three years, and (3) July-September of the previous three years. Correlations were higher if the data for each period were weighted so that those of the ealier years had less influence on the total. Weighting consisted of adding

together the temperature of the previous year, one half of the temperature of the year before and one quarter of the temperature of the year before that.

The best overall correlation was obtained with the weighted mean temperature during July-September of the previous three years (Table I).

Precipitation

The detailed investigation was confined to a consideration of the total precipitation as preliminary investigations showed that this gave a generally higher correlation than either the heaviest fall of the month or the number of days on which rain fell.

Correlation coefficients were calculated between grasshopper density and total precipitation for 81 different periods between January and December during the same and up to six preceding years. Of these, the highest correlations – which were both negative – were obtained with total precipitation during (1) April-August of the previous two years, and (2) April-August of the previous three years (Table II). Weighting the data so that previous years had less influence on the total did not increase the correlation coefficients. There is evidence that the more northern areas show a higher correlation with precipitation during the previous three years than with precipitation during the previous two years, but these differences are not significant and there can be no justification at this stage for subdividing the Province into two regions.

Discussion

The evidence supplied by this work supports the view put forward by Parker (1933) that there is an association between grasshopper populations and mean monthly temperature during July-September of the previous three years. There is evidence of a weaker relationship between grasshopper populations and total precipitation during the period April-August of the previous two years.

The close relationship between grasshopper densities and hot dry weather is shown in Fig. 2, which refers to R.M. 159 (Regina). Since 1930 there have been four periods when the weighted total of the mean monthly temperatures during July-September in three consecutive years has been above normal. During each of these periods – and only during these periods – the average density of grasshoppers in the Rural Municipality has also risen above normal. There is a less well defined inverse relationship between grasshopper density and total precipitation during April-August of two consecutive years.

The devastating grasshopper outbreaks of 1932-1935 and 1938-1939 were associated with conditions of high temperature and low precipitation which have never occurred since. The lesser outbreaks of 1949 and 1959 were associated with periods when precipitation was sub normal but when the temperature excesses were less and of shorter duration.

This association between grasshopper densities and weather conditions has persisted in spite of vigorous control campaigns in certain years and in the face of continually changing cultural practices. Vigorous control campaigns reduce the number of grasshoppers in the year in which they are applied, and hence reduce the amount of crop damage in that year, but they appear to have had no marked effect on the overall relationship between grasshopper densities and weather conditions during the period of this study.

Although the correlation between grasshopper densities and weather conditions is very high this is no proof of a cause-and-effect relationship. Even if such a relationship is assumed we cannot say, at the present state of knowledge, whether this effect is brought about by the direct action of weather on the

TABLE I

Correlation between grasshopper density and mean monthly temperature in Saskatchewan 1935-1958. The temperature figures have been weighted so that the most recent year has the greatest influence (See text).

Weather station	Pairs of observations	During the previous three years		
		July	June – September	July – September
North Battleford	24	.757***	.747***	.768***
Macklin	21	.462*	.648***	.663***
Scott	22	.720***	.622**	.599**
Biggar	20	.629**	.543**	.539**
Kindersley	21	.440*	.529*	.607**
Saskatoon	23	.578**	.478*	.465*
Outlook	22	.516**	.783***	.790***
Leader	20	.678***	.814***	.827***
Beechy	13	.555*	.827***	.848***
Swift Current	20	.334	.512*	.618**
Shaunavon	17	.609*	.506*	.668**
Assiniboia	16	.642**	.588*	.772***
Davidson	21	.516*	.647***	.640**
Nokomis	20	.591**	.478*	.754***
Moose Jaw	23	.602**	.650***	.643***
Regina	24	.628**	.770***	.838***
Indian Head	24	.688***	.827***	.844***
Yellow Grass	24	.660***	.751***	.718***
Midale	23	.773***	.634***	.688***

* Significance at 5% level of confidence
** Significance at 1% level of confidence
*** Significance at 0.1% level of confidence

TABLE II

Correlation between grasshopper density and total precipitation in Saskatchewan, 1935–1958.

Weather station	Pairs of observations	During April-August of the previous	
		Two years	Three years
North Battleford	24	−.582**	−.726***
Macklin	21	−.523*	−.587**
Scott	22	−.472*	−.650***
Biggar	20	−.658**	−.736***
Kindersley	21	−.421	−.357
Saskatoon	23	−.454	−.432*
Outlook	22	−.502*	−.423*
Leader	20	−.411	−.402
Beechy	12	−.729**	−.630*
Swift Current	20	−.516*	−.494*
Shaunavon	17	−.570*	−.606**
Assiniboia	16	−.397	−.102
Davidson	20	−.493*	−.475*
Nokomis	20	−.561**	−.586**
Moose Jaw	23	−.606**	−.543**
Regina	24	−.822***	−.680***
Indian Head	24	−.661***	−.639**
Yellow Grass	24	−.636**	−.545**
Midale	23	−.750***	−.658***

* Significance at 5% level of confidence
** Significance at 1% level of confidence
*** Significance at 0.1% level of confidence

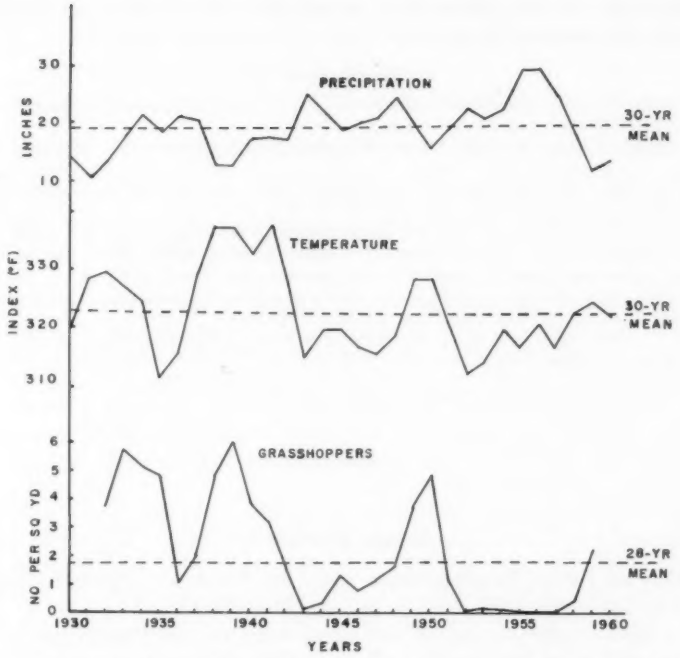

Fig. 2. Relationship between grasshopper densities, temperature and precipitation in R.M.159 (Regina). Grasshopper densities refer to the years shown. Temperatures refer to the total mean monthly temperature during July-September of the previous three years, weighted by the method described in the text. Precipitation refers to the total precipitation during April-August of the previous two years.

grasshoppers' physiology, by its indirect action on their food plants, or by a differential effect on their predators, parasites and diseases. Research on these aspects is urgently needed and would likely be very profitable, not only by shedding light on a fundamental problem in population ecology but also as a necessary prerequisite to adequate long-term control measures.

What can be said at the present time is that provided the relationship between grasshoppers and weather factors remains the same in the future as it has in the past, there is a good chance that weather data may be useful in predicting grasshopper outbreaks. Work along these lines is already well advanced.

Summary

Grasshopper populations in nineteen areas of Saskatchewan during each of the past twenty-five years have been compared with weather conditions in the preceding years. Correlation with weighted mean monthly temperature during July-September of the previous three years was highly significant. Correlation with precipitation during April-August of the previous two years was significant in most areas.

Acknowledgments

I wish to express my thanks to past and present staff of the Entomology Section, of the Canada Agriculture Research Station, Saskatoon, who compiled

the grasshopper survey sheets, and to my wife who tabulated most of the population and weather data.

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Book Review

Physiology of Insect Development, edited by Frank L. Campbell, University of Chicago Press, 1959. XIV + 167 pp. Price $4.00.

This book is the record of the Conference of the Physiology of Insect Development held at Macdonald College in 1956, immediately before the International Congress of Entomology. The conference was one of a series on developmental biology sponsored by the National Academy of Sciences; the chairman was Dr. Max Day of Canberra and there were some twenty distinguished participants, from North America, western Europe and Australia. A distinctive feature of the book is that it is essentially a transcript of the discussions, recorded on tape at the time and later edited to yield an orderly and readable text. Thus each chapter (session) includes contributions from many participants who are engaged in reporting, discussing and criticizing recent researches in a particular field. It is evident that the conference achieved its aim of bringing a great diversity of experience to bear on the discussion of the various developmental processes, and by skillful editing much of this stimulating exchange of thought has been preserved for the reader. One must not expect, of course, to find any organized review of recent advances; the procedure is rather that a subject is introduced by an active worker in the field and his case is then examined or extended by others, often of very different background. But the conference was so interesting, and the reporting so well done, that the book may either be read continuously, as an account of recent work and thoughts in various active fields of research, or sampled as an anthology of wise or stimulating sayings whose value may not be quickly exhausted ('I do not think insect blood is the intercellular fluid of insects. No one knows what it is').

The subject of the Conference was discussed under eight main heads, embryology, larval development, tissue culture, metamorphosis, diapause, histolysis, tumours and regeneration. With so much to choose from it is both difficult and invidious to select items for comment, but the book may be very confidently recommended to all who are interested in the physiology and development of insects.

J. A. Downes

Notes on the Family Odiniidae with a Key to the Genera and Descriptions of New Species (Diptera)

By G. E. SHEWELL
Research Branch, Canada Department of Agriculture, Ottawa, Ontario

The genera comprising the family Odiniidae (Hendel, 1922) will run to Agromyzidae in the key to families in Curran (1934), but are distinguished from this family by a number of important characters, notably the abdominal structure of the adult and the bucco-pharyngeal skeleton of the larva. Adult Odiniidae have five pregenital abdominal segments in both sexes. The sixth segment of the female is greatly reduced and largely hidden beneath the fifth, and the seventh is membranous and retractile. In Agromyzidae six well-developed pregenital segments are present and the seventh segment of the female is modified as a heavily-sclerotized non-retractile ovipositor. The odiniid larva (Figs. 2, 6.) has a mouth skeleton much like that of the more generalized saprophagous forms (e.g. *Drosophila*, *Piophila*, *Lucilia*) and in no way resembling the highly-specialized structure of Agromyzidae. Species of Odiniidae are pale grey or clay-yellow with the thorax and abdomen conspicuously mottled or vittate with dark brown. The wing is usually spotted, at least on the cross-veins, and the tibiae have a more or less evident preapical dorsal bristle. Because of the abdominal structure, Hennig (1938) considers them more closely related to Chamaemyiidae than to Agromyzidae. The immature stages have mostly been found living in the galleries of wood-boring Coleoptera and Lepidoptera but the adult of *Turanodinia* Stack. is reported to have been reared from egg-masses of *Pseudococcus comstocki* Kuw.

Key to genera of Odiniidae

1. Disc of scutellum haired 2
   Disc of scutellum bare 4
2. Ocelli on large tubercle well forward of vertex 3
   Ocelli normal. Frons not tuberculate (Neotrop., Palaearct.) ..... *Schildomyia Mall.* (1926)
3. Arista long-plumose. Fourth vein strongly curved forward at apex (Neotrop.) ..... *Paratraginops* Hend. (1917)
   Arista pubescent. Fourth vein straight. (Holarct., Neotrop., Orient.) ..... *Traginops* Coq. (1900)
4. Five dorsocentrals. Mesopleuron bare 5
   Four dorsocentrals. Mesopleuron haired (Holarct.) ..... *Neoalticomerus Hend.* (1903)
5. Posterior crossvein absent, replaced by dense patch of microtrichia (Palaearct.) ..... *Turanodinia* Stack. (1944)
   Posterior crossvein present (Holarct., Neotrop.) ..... *Odinia* R.-D. (1830)

Paratraginops Hend.

Hendel, F. 1917. *Deutsch. Ent. Ztschr.* 1917, p. 38.

Hendel evidently relied solely on the description of *Traginops pilicornis* Cress. (1912) for his generic diagnosis. Examination of paratypes of *pilicornis* shows that, of the four characters listed by him as distinguishing the genus from *Traginops* Coq., two must be eliminated. Cresson stated that *pilicornis* possessed only one pair of dorsocentral bristles, but there are, in fact, four pairs as in *Traginops irrorata* Coq. In *pilicornis*, these bristles are progressively weaker anteriorly, so that the presutural pair is about half the size of the hindmost pair. The shape of the scutellum in *pilicornis*, its convexity, and particularly the slightly tuberculate apex is also closely matched by that of *irrorata*. The remaining two characters distinguishing *Paratraginops*, namely the very long-plumose arista and the strongly narrowed apex of the first posterior cell are, however,

important enough for generic separation of *pilicornis*, at least provisionally. To them may be added its distinctive wing pattern and much larger size.

Type species *Traginops pilicornis* Cresson, 1912, British Guiana.

Key to species of *Paratraginops*

Anterior four frontal bristles not set in fuscous spots. Base of scutellum thickly haired. Marginal cell of wing entirely dark ..... *pilicornis* Cress.
Anterior four frontals set in fuscous spots. Base of scutellum bare. Marginal cell broadly pale in middle ..... *plaumanni* n.sp.

***Paratraginops plaumanni* n.sp.**

(Fig. 1)

Head and thorax dull brownish-yellow, faintly grey-pruinose, mottled and vittate with dark brown. Scutellum with conspicuous pale yellow median vitta. Abdomen shining dark chocolate brown with pale cinereous markings. Legs light reddish brown with dark brown markings. Wing darkened at base, on crossveins, and at apex. Length of body 5.0-6.0 mm., of wing 5.5 mm.

Head slightly broader than anterior part of thorax, in profile subrectangular, twice as high as long. Upper half of frons dark brown including prominent ocellar tubercle which is midway between vertex and antennae; orbits, haired portion of cheeks, and two narrow stripes from posterior ocelli to inner verticals pale golden-pollinose; frontal bristles set in fuscous spots; lunule pale cinereous-pollinose with large velvet-black spot; antennal – and cheek grooves and upper occiput laterally darker brown. Antenna yellow, third segment noticeably paler; arista mostly black, loosely long-plumose above and below, shorter plumose on inner surface. Palpus yellow; theca light brown. Two or three pairs of well-developed divergent postverticals surrounded by numerous shorter hairs; a dense patch of proclinate hairs between vertex and ocellar tubercle; ocellars strong, divergent, proclinate; three to five strong peristomal bristles behind vibrissa and, behind them, two or three strong upcurved genoorbitals; a row of about six strong decumbent bristles near posterior margin of cheek.

Thorax with dark drown markings as follows: A broad middorsal vitta narrowing to a point at scutellum; elongate spots at bases of dorsocentral bristles, sometimes confluent with middorsal vitta; large spots beside humerus and at base of presutural bristle; a broad elongate spot at base of intraalar and inner postalar bristles and, in front of this, a narrower vitta running forward to suture and then following suture a short distance medially; small spots at bases of humeral and notopleural bristles; a narrow vitta enclosing bases of supraalar and outer postalar bristles; two broad lateral vittae on scutellum passing between the bristles and continuing on ventral surface; three vittae crossing mesopleuron, upper one commencing on underside of humerus and continuing to root of wing, middle one continued on upper edge of pteropleuron, lower one covering base of propleural bristle, margins of upper two vittae strongly sinuous; a short median vitta on pteropleuron; an obscure vitta below sternopleural bristles. Chaetotaxy: 1 + 3 dorsocentrals, 1 prescutellar acrostical, 4 scutellars, 1 humeral, 1 presutural, 1 intraalar, 2 supraalars, 2 postalars, 2 notopleurals, 1 propleural, 1 stigmatal, 3 sternopleurals. Acrostical hairs in about 12 rows. Scutellum thickly haired except basally and on middorsal line. Wing (Fig. 1) fumose, especially at base and apex of submarginal cell and on anterior crossvein. A broad hyaline area from end of first vein to beyond posterior crossvein and from costa to fifth vein, enclosing clouded crossveins. Veins yellowish-brown in hyaline areas of wing, elsewhere dark brown. Fourth vein strongly curved forward at apex. Squama fumose. Haltere brownish-yellow. Legs light reddish-yellow with the follow-

ing dark brown areas: Anterior surface of fore coxa; anterior and posterior surfaces of fore femur except narrow base and broad apex, dark marks confluent apically below; an oblique preapical mark on anterior and ventral surfaces of mid- and hind femur; subbasal and preapical rings on all tibiae; apical two or three segments of tarsi.

Hind margins of second to fourth abdominal tergites laterally with narrow scalloped cinereous bands which, on reaching the recurved ventral surface become pale golden-pollinose and turn obliquely forward so as to leave the posterolateral corner dark. Fifth segment with similar markings but the cinereous portion of the band much broader and discontinuous with the golden portion below.

Holotype, ♂, *Allotype*, 5 *Paratypes*, Nova Teutonia, S. Brazil, 300 - 500 m. II - III. 1959. Fritz Plaumann. C.N.C. No. 7124.

Note. P. pilicornis (Cress.) has the following distinguishing characters besides those given in the key above. Ground colour of thorax darker, somewhat cinereous; middorsal vitta continuing broadly to scutellum; elongate spots confluent between second and third dorsocentral bristles; spot at base of intraalar fused with the vitta in front of it; dorsocentral bristles progressively weaker anteriorly (not so in *plaumanni*); acrostical hairs in about 16 rows and very noticeably denser in prescutellar area; scutellum pale yellow only at extreme tip; lower part of thorax, coxae, and most of femora dark brown.

Traginops Coq.

Coquillett, D. W. 1900. *Ent. News.* 11: 429.

Differs from *Paratraginops* in its smaller size, pubescent arista, straight fourth vein, and spotted or reticulate wing pattern. However, *T. clathrata* Hend. from S. America possesses the following characters that are akin to *Paratraginops* rather than to the type species. Ocellar tubercle less pronounced; lunule with velvet-black spot; mesonotal pattern very like *P. plaumanni* n.sp., with large dark brown spots and vittae, hairs not set in small round spots; acrostical hairs in about 10 rows; scutellum thickly haired over most of dorsal surface; strong stigmatal bristle present. Hendel (1909) evidently noted the stigmatal bristle in his one or two specimens and in recharacterizing *Traginops* wrote cautiously "*Eine (vielleicht abnormal zwei) starke Prothorakalborste*". All the specimens of *clathrata* before me have the stigmatal well developed.

Type species, *Traginops irrorata* Coquillett, 1900. Georgia, U.S.A.

Key to species of *Traginops*

1. Stigmatal bristle present. Lunule with velvet-black spot (Neotrop.) ..... *clathrata* Hend. (1909)
   Stigmatal bristle absent. Lunule unspotted 2
2. A distinct dark brown spot on orbit near posteroventral corner of eye and, anterior to it, a smaller elongate spot (Nearct.) ..... *irrorata* Coq.
   No such spots on orbit 3
3. Fore tarsus blackish brown; hind metatarsus except at base and apex blackish brown (Orient.) ..... *orientalis* de Meij. (1911)
   Tarsi brownish yellow (Palaearct.) ..... *orientalis naganensis* Kato (1952)

Traginops irrorata Coq.

(Figs. 2 - 4)

Coquillett, D. W. 1900. *Ent. News.* 11: 429.

Larva Mouth hooks slender, with very prominent posterodorsal process. Complex labial and subhypostomal sclerites present. Ventral cornu of pharyngeal sclerite near base with slight protrusion and near apex with a small oval pigmented area; dorsal cornu slender.

Puparium Length 3.7 mm. Width 1.0 mm. Light yellowish brown; in cross-section subovate, venter not much flattened; segmentation indistinct except anteriorly. Anterior spiracles on short divergent stalks narrowly separated at base; each spiracle with five to eight short branches arranged fanwise. Transverse line of cleavage (hinges of opercula) at posterior third of first abdominal segment. Posterior spiracles widely separated on a small tubercle. (Described from a single specimen on which the drawing of the larval mouth skeleton is also based).

As remarked by Kato (1952) the differences between *orientalis* de Meij. and *irrorata* are so slight that, when properly compared, these forms may prove identical. I have not seen examples of *orientalis* but, on the basis of Kato's excellent description and figures of his subspecies *naganensis*, I note the following differences from *irrorata* besides those given in the key above. In *irrorata* the frontal bristles are evenly spaced, and the fuscous spots at bases of the upper two pairs are, in lateral view, either confluent or separated only by a very narrow pale pollinose line. The third antennal segment is entirely pale, without any suggestion of a faint brown mark below base of arista. The posterior four femora have, at the apical third, a very conspicuous oblique dark brown bar on the anterior and ventral surfaces, this mark being noticeably darker than the grey-pollinose basal third or more of the femur. De Meijere (1911) mentions such a mark (*vor der Spitze unten ein dunkelbrauner Halbring*) only for the hind femur of *orientalis*, describing the middle femur as *ganz gelb, nur unten an der wurzel und vor der Spitze etwas graulich*. In *irrorata*, all the metatarsi are dark brown except at base and apex, the following three segments are pale and the last dark brown (Compare characters of *orientalis* and *naganensis* given in the key above).

Material in C.N.C. 20 ♂♂, 36 ♀♀ from the following localities. QUE. Hemmingford (Curran, Petch); La Trappe (Ouellet). ONT. Ottawa, reared 28. VII. from puparium in exuding wound on trunk of *Ulmus americana*. Adults at same wound (McAlpine); Bell's Corners, at sap on stump of *Acer saccharum* (McAlpine); Black Rapids, near Ottawa, (Ide); Niagara Glen (Walley). MASS. Fall River, at sap of *Quercus* (Johnson). Most specimens in June and July, a few in August.

Traginops clathrata Hend.

Hendel, F. 1909. *Wien Ent. Ztg.* 28: 52.

Type locality: Vilcanota, Peru

Material in C.N.C. 9 ♂♂, 9 ♀♀, Nova Teutonia, S. Brazil. 300 - 500 m. Nov., Jan. and Feb. (Plaumann).

Neoalticomerus Hend.

Hendel, F. 1903. *Wien Ent. Ztg.* 22: 252.

Postocellars very small, slightly proclinate; vibrissa well above anterior oral margin; anterior peristomal bristle not much weaker than vibrissa and placed below it. Mesonotum with four dorsocentrals (one before suture), one intraalar, and one very small prescutellar acrostical. Sometimes a weak stigmatal bristle present. Mesopleuron with scattered hairs above and with one or two strong bristles posteriorly. Hind legs of both sexes normal, those of male not shortened and incrassate. Otherwise similar to *Odinia* R.-D.

Type species, *Milichia formosa* Loew, 1843. Posen, Germany (now Poznan, in Poland).

(This genus has not previously been reported from N. America)

***Neoalticomerus seamansi* n.sp.**

(Figs. 5 - 11)

Cinereous pollinose. Thorax vittate and abdomen puntate with dark brown. Crossveins of wing clouded. Legs uniform dark brown. Length of body 3.0 mm., of wings 3.0 mm.

Head cinereous; broad frontalia darker grey or brown, anterior margin reddish-yellow; ocellar triangle large, two-thirds length of frons; bristles set in dark brown spots. Lunule and upper half of face and parafacials dark brown; lower half of face and bare upper part of genae pale cinereous, almost niveous. Vibrissal angle almost midway between anterior oral margin and level of ventral margin of eye. Antennal bases separated by a distance about equal to length of second segment; antenna dark brown, third segment below a little paler; arista micropubescent. Mouthparts, including palpus, dark brown; clypeus shining.

Thorax cinereous above; mesonotum with a narrow median dark brown vitta from about in line with anterior dorsocentral bristle almost to apex of scutellum, and with a similar but slightly broader vitta from above humerus to postalar callus passing over upper part of notopleuron and enclosing presutural, supraalar, and outer postalar bristles; dorsocentral bristles set in dark brown spots which are sometimes more or less confluent forming very narrow vittae; acrostical hairs sparse, in six or eight irregular rows, outer rows with only a few hairs; one or two irregular rows of sparse hairs and sometimes also a faint brown streak in front of intraalar bristle. Pleura with a broad dark brown vitta from lower surface of humerus almost to base of haltere, leaving posterodorsal corner of mesopleuron and adjacent part of pteropleuron pale. Lower margin of mesopleuron and entire sternopleuron dark brown. Wing membrane milky, veins pale brown; costal break and base of third vein darkened; both crossveins with brown cloud; second and third veins very little divergent; subcostal cell apically little more than half width of first posterior; penultimate section of fourth vein, posterior crossvein and ultimate section of fifth subequal. Squamae, including fringe, white. Haltere white. Legs dark brown; tibiae with preapical dorsal bristles, mid-tibia with two equal ventral spurs.

Abdomen cinereous-pollinose; third to fifth segments each with a narrow middorsal vitta and a pair of anterolateral spots dark brown. Male hypopygium small, shining dark brown with ovate styles.

Larva. Length 5.0 mm. White; slender; consisting of 12 segments; broadest at fourth or fifth abdominal segment; last segment rounded-truncate. Pseudocephalon anteriorly with two pairs of small sensory papillae. Margin of oral cavity with dense tufts of microsetae anteriorly and with four or five oblique rows each of about 12 minute retrorse spines. Mouth hooks robust. Accessory ventral sclerites, except the dentate, absent. Ventral cornu of pharyngeal sclerite with prominent subbasal protrusion and with heavily-pigmented oval area near apex. Anterior spiracle with 11 or 12 branches arranged fanwise. Second to seventh abdominal segments with ventral spinous locomotory pads; spines in two close-set groups each of two proclinate rows followed by three reclinate rows; second group, except first and last rows, consisting of much larger spines. Posterior spiracular plate flush with body wall; slits oval; chamber constricted towards base. (Described from a single specimen).

Puparium Length 3.7 mm. Width 1.0 mm. Castaneous; in cross-section subovate; segmentation distinct, articulations between segments more or less constricted. Anterior spiracles prominent, their bases very widely separated. Transverse line of cleavage at about posterior third of first abdominal segment.

Dorsum of eighth abdominal segment with distinct longitudinal groove. Posterior spiracles prominent, well separated on a moderately large tubercle.

Holotype, ♂, and *allotype*, Lethbridge, Alta. June 6 1923, H. L. Seamans. C.N.C. no. 7125.

Paratypes, 3 ♀ ♀, Rivière des Caches, Northumberland Co., N.B. Forest Insect Survey No. 59-1240-01. Emerged Aug. 12, 1959 from puparia taken July 27 from galleries of *Cryptorhynchus lapathi* (L.) (Curculionidae) in stem of large *Populus balsamifera*. One larva found adhering to one of above puparia. One puparium and the larva mounted on slide.

Note. The types have been compared with a male and two female specimens of *N. formosus* (Lw.) from Sondria, Italy, in the U.S.N.M. The European species has 10 - 12 rows of acrostical hairs and 3 - 4 rows of lateral hairs on the mesonotum. The middorsal vitta is also somewhat broader than in *seamansi* n.sp. The abdomen is shining brown on most of segments 1-4, which are thickly pollinose only on the lateral and posterolateral margins. In oblique view, a thin covering of grey pollen is seen except on the large brown laterobasal spots of each segment. Fifth segment grey-pollinose with a broad middorsal vitta and large lateral spots brown (The above abdominal characters correspond closely with Loew's (1853) description). Frons more extensively reddish and much less thickly pollinose than in *seamansi*. Genital styles shorter and paler.

It is a pleasure to name this species for Mr. H. L. Seamans, formerly Head, Field Crop Insect Unit, Entomology Division, Ottawa, and for many years in charge of the Field Crop Insects Laboratory, Lethbridge.

Odinia R.-D.

Robineau-Desvoidy, J. B. 1830. Essai sur les Myodaires. p. 648.

Type species, *Odinia trinotata* R.-D. = *Milichia maculata* Mg. (1830). Saint Sauveur, France.

Thirteen species and one subspecies are now recognized. Collin (1952) and Sabrosky (1959) have recently published reviews of the European and Western Hemisphere species respectively. Sabrosky has recognized two holarctic species and I can now report a third.

Odinia xanthocera Coll.

Collin, J. E. 1952. *Proc. R. Ent. Soc. London. B.* 21: 112.

Type data not given, but the species is said to occur in the galleries of *Cryptorhynchus lapathi* L. in twigs of *Alnus*, *Salix*, and *Populus* in Europe.

Three male and one female specimen from B.C. differ from Collin's description only as follows: Frons anteriorly reddish-yellow, faintly cinereous-pollinose. Each lateral pair of spots on third abdominal segment narrowly connected behind. Fore femur posteriorly and hind femur anteriorly dark brown (not uniform in

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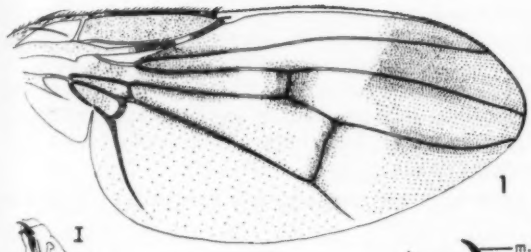
Fig. 1. *Paratraginops plaumanni* n.sp. Wing, x 14.5.

Figs. 2-4. *Traginops irrorata* Coq. 2. Larva; buccopharyngeal skeleton. 3. Puparium; dorsal view, x 19. 4. Anterior spiracles.

Figs. 5-11. *Neoalticomerus seamansi* n.sp. 5. Larva, x 19. 6. Bucco-pharyngeal skeleton. 7. Anterior spiracle. 8. Spines of locomotory pad of fifth abdominal segment. 9. Posterior spiracle. 10. Puparium; dorsal view, x 19. 11. Wing, x 14.5.

Figs. 12, 13. *Odinia brevitibia* n.sp. 12. Wing, x 14.5. 13. Hind leg.

(*p.s.p.*, posterior spiracular plate; *cl*, cleavage line of operculum; *dc*, dorsal cornu; *dt*, dentate sclerite; *hp*, hypostomal sclerite; *lab*, labial sclerite; *m.h.*, mouth hook. *p*, subbasal protrusion of ventral cornu; *pdp*, posterodorsal process of mouth hook; *ph*, pharyngeal sclerite; *psc*, pseudocephalon; *pst*, parastomal sclerite; *shp*, subhypostomal sclerite; *vc*, ventral cornu.)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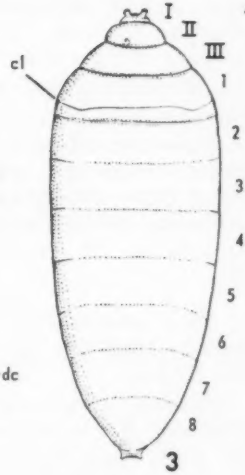

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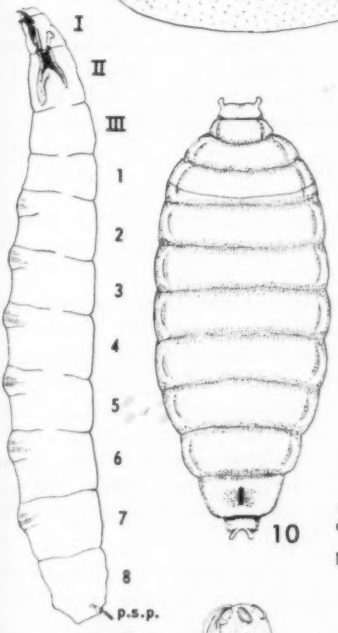

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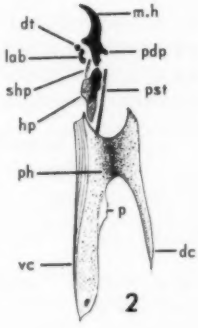

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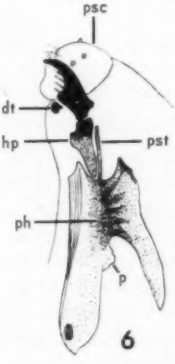

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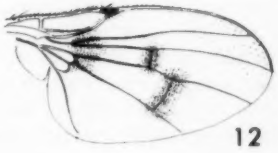
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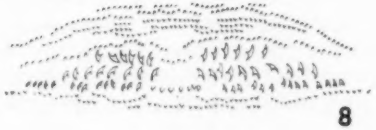
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all specimens). Hind tibia with distinct subbasal dark ring. Only the female specimen with a small brown spot on third antennal segment.

This species will be difficult to separate from *Odinia boletina* (Zett.) unless the colour of the frons and antenna is a reliable character. No males referable to *boletina* are yet known from N. America. The female specimens identified as this species by Sabrosky (1959) have the frons entirely grey (a character of *xanthocera* according to Collin) and the second antennal segment brownish yellow, although the tip, and in some lights the entire segment, appears hardly darker than the third. The latter, however, has a large brown spot on both sides extending to the anterior margin.

Collin (1952) says that *boletina* is associated with a fungus on *Populus* in England.

Material in C.N.C. ♂, ♀, Cowichan, B.C. 8 - 11. Aug. 1959. Reared from puparia in mines of *Cryptorhynchus lapathi* (L.) in *Salix*. ♂, Cowichan L., B.C. 24 Aug. 1959. Emerged into cage containing Salix stems infested with *C. lapathi*. ♂, Nanaimo, B.C. 15 Sept. 1959. Reared from larva in mine of *C. lapathi* in *Salix*.

***Odinia brevitibia* n.sp.**

(Figs. 12, 13)

Third antennal segment very small. Crossveins broadly and conspicuously clouded. Hind tibia of male extremely short. Length of body 3.0 mm., of wing 3.0 mm.

Frontalia dark brown, anterior margin dull reddish, thinly greyish–or yellowish-pollinose, with a waxen sheen, sparsely haired anteriorly, bare on sides above, hairs minute; ocellar triangle and orbits more thickly pollinose, latter becoming silvery anteriorly; insertions of bristles, including ocellars and postocellars, shining black. Lunule black to lower edge of antennal sockets. Face, cheeks, and lower occiput silvery-pollinose. Upper occiput darker, more yellowish. A single strong peristomal bristle behind vibrissa; cheek bristles sparse and weak. First two antennal segments brown, third segment reddish orange, very small, not longer than distance between anterior and posterior ocelli; arista black, micropubescent. Palpus reddish orange.

Thorax pale grey-pollinose, disc and scutellum more brownish or yellowish, upper half of pleura more silver. Mesonotum with only an obscure narrow middorsal vitta incomplete behind; bristles set in dark spots. Upper pleura immaculate or with a very faint vitta above; sternopleuron dark brown, dull grey-pollinose. Chaetotaxy normal; acrostical hairs in about eight irregular rows. Wing with apex of first vein and both crossveins very conspicuously clouded, also a dark band from middle of first vein to apex of second basal cell; apical half of wing slightly fumose with tips of veins darkened; crossveins separated by less than length of posterior crossvein; squama including fringe pale. Haltere pale brownish yellow, knob whitish. Legs including coxae dark brown; inner surfaces of fore and hind femora, apices of all femora and bases of all tibiae and a very obscure ring beyond middle of fore and mid tibiae brownish yellow; mid tibia with two subequal ventral spurs; hind tibia extremely short, reaching only halfway to base of femur, its dark apical portion only half length of tarsus, latter expanded towards apex, pulvilli white.

Abdomen greasy, pollen pattern obscured; ground colour dark with narrow apices of segments paler.

Type, ♂, Nova Teutonia, S. Brazil, 300 - 500 m., IX. 1958, Fritz Plaumann. C.N.C. No. 7126.

Summary

The European genus *Neoalticomerus* Hend. and the species *Odinia xanthocera* Coll. are recorded from N. America for the first time. The following new species are described: *Neoalticomerus seamansi* from Canada, *Paratraginops plaumanni* and *Odinia brevitibia* from Brazil. The hitherto unknown immature stages of *Traginops* Coq. and *Neoalticomerus* are described. Keys to the genera of Odiniidae and to the species of *Traginops* and *Paratraginops* Hend. are given, with notes on the value of some characters used by previous authors.

Acknowledgments

I am indebted to the authorities of the Academy of Natural Sciences of Philadelphia, through Dr. Harold J. Grant Jr., for the loan of paratypes of *Paratraginops pilicornis* (Cress.), and to the United States National Museum, through Mr. C. W. Sabrosky for permission to examine specimens of *Neoalticomerus formosus* (Lw.). Dr. D. C. Eidt, Forest Biology Laboratory, Fredericton, N.B. and Mr. J. W. E. Harris, Forest Biology Laboratory, Victoria, B.C. very kindly supplied biological information and specimens of *N. seamansi* and *O. xanthocera* respectively.

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Addendum

Since preparing the descriptions of *Paratraginops plaumanni* and *Neoalticomerus seamansi* n. spp., I have seen the following additional specimens and, after comparing them with the original series, hereby designate them paratypes. *P. plaumanni*: Rio de Janeiro, Brazil, Jun. Jul. 1938. Servico Febre Amarela. M.E.S. 1 ♂, 1 ♀. Juquia, S. Paulo, Brazil VI. 38. J. Lane. 1 ♂. (U.S.N.M.) *N. seamansi*: Chadron, Nebr., Aug. 20, 1950, M. R. Wheeler, 2 ♀ ♀; Patagonia, Ariz., June 15, 1951, M. R. Wheeler, 1 ♂, 1 ♀. (Collection of M. R. Wheeler, Austin, Tex.)

(Received April 22, 1960)

Notes on the Occurrence and Morphology of *Bryobia lagodechiana* Reck in British Columbia (Acarina: Tetranychidae)[1]

By C. V. G. Morgan

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Summerland, British Columbia

Bryobia lagodechiana Reck, 1953, was originally found on bedstraw, or cleavers, *Galium* sp., growing at an elevation of about 6,890 to 7,220 feet above sea level in the Lagodekhsky reserve of the Armenian S.S.R. (Reck, 1953; Bagdasarian, 1957). A mite believed, on the basis of illustrations and descriptions only, to be the same species was found by the author in one locality in the Okanagan Valley of British Columbia. It was first observed on June 6, 1958, when about 10 female mites were noticed feeding on common horsetail, *Equisetum arvense* L., growing at an elevation of 3,300 to 3,500 feet near Orofino Creek on Mount McCaig, known locally as Orofino Mountain. The site, which was partially shaded by fairly heavy stands of tall coniferous trees, was somewhat boggy, and would undoubtedly be flooded during the spring run-off of Orofino Creek. Luxurious pure stands of this horsetail are common in such sites and, except for moss, it is often the predominant plant in many creek-bottom areas. An additional 20 female mites were collected at the same site on June 12, 1958. No males, or immature stages, were seen on either date. This is the first record outside southern Russia of the occurrence of a mite closely resembling *B. lagodechiana*, and the first report of the occurrence of any species of *Bryobia* on plants of the family Equisetaceae. The slide-mounted specimens are in the Canadian National Collection.

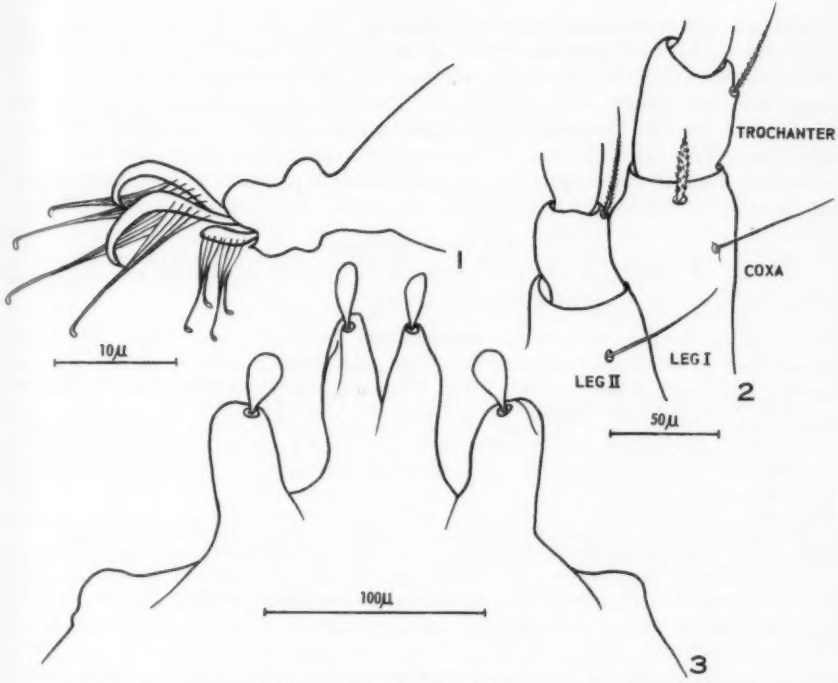
B. lagodechiana is readily distinguished from all other species of the genus *Bryobia* by the number of tenent hairs on empodium I, the shape of the propodosomal lobes, the relative lengths of the foreleg and the body, and the position of the three pairs of dorsocentral hysterosomal setae.

Only two other *Bryobia* species resemble *lagodechiana* in the two pairs of ventrally directed tenent hairs borne on empodium I: *eharai* Pritchard and Keifer, 1958, apparently native to Asia and intercepted at Seattle, Wash., on imported chrysanthemums; and *artemisiae* Bagdasarian, 1951, found only in southern Russia. All other species have either one pair or more than two pairs. In *lagodechiana* empodium I is a pad-like structure about four microns long (Fig. 1). Each tenent hair is supported by four roots, or small hairs, which arise from the lateroventral surface of the pad and coalesce about their midlength. The tenent hairs of the claws of leg I arise from five roots. The finger-like empodia II to IV are each about 15 microns long and bear two rows of ventrally directed tenent hairs; each row consists of at least 10 hairs. All tenent hairs are posteriorly bent at right angles and somewhat enlarged at the tip to form a very small, glandular-like pad.

The propodosomal lobes of *lagodechiana* are distinctively shaped (Fig. 3). The outer pair are teat-like; the sides are parallel, and the tip is smoothly rounded or somewhat flattened. The foliaceous setae, borne on these lobes, characteristically arise mesad of the tip and are directed towards the inner lobes. A wide, deep depression separates the outer and inner lobes. The inner lobes are somewhat pointed and extend well beyond the setae of the outer pair. The setae of the inner lobes are definitely narrower than the setae of the outer lobes.

The propodosomal anterior angulations arise just proximad of the propodosomal lobes and are strongly developed.

[1]Contribution No. 11, Research Station, Research Branch, Canada Department of Agriculture, Summerland, British Columbia.



Figs. 1-3. *Bryobia lagodechiana* Reck in British Columbia. 1, tenent hairs, claws, and empodium of leg I (tarsal setae not shown); 2, coxa and trochanter of legs I and II; 3, propodosomal lobes and propodosomal anterior angulations (setal spines not shown).

Unlike the forelegs of most other species of *Bryobia* those of *lagodechiana* are much longer than the body. This characteristic alone distinguishes *lagodechiana* from *artemisiae* and *eharai*. In *artemisiae* the forelegs are shorter than the body (Bagdasarian, 1951); in *eharai* the lengths of the foreleg and body are similar (Pritchard and Keifer, 1958). In his description of *lagodechiana*, Reck (1953) stated that the foreleg is 910 microns long and the lengths of the individual segments are: tarsus, 155; tibia, 260; genu, 75; and femur, 370 microns. As the sum of these segments is only 860 microns, Reck must have included part or all of the trochanter in the total length of the foreleg. Based on 25 adult female mites, the average length of leg I of *lagodechiana* found on horsetail in British Columbia is 848 ± 25 microns. The individual segments measure: tarsus, 136 ± 5; tibia 250 ± 11; genu, 86 ± 2, femur, 319 ± 10; and trochanter, 57 ± 3 microns. The length and width of the body of these specimens are 768 ± 26 microns and 444 ± 22 microns respectively. Corresponding measurements given by Reck are 750 and 445 microns.

Coxa I of *lagodechiana* on horsetail bears two setae; the inner one is long and setiform, and the outer one, which lies anterolaterad of the inner one, is much shorter, somewhat foliaceous, and beset with spines (Fig. 2). Coxae II to IV each bear only one seta, which is long and setiform. Only one seta is borne on each trochanter; the first two are long and plumose but those on legs III and IV resemble the outer seta of coxa I.

The three pairs of dorsocentral hysterosomal setae are borne on short tubercles near the mid-dorsal region of the body. Based on measurements of

25 females collected from common horsetail, the setae of the DC_1 pair are separated by 86 ± 5 microns, those of the DC_2 pair by 76 ± 7 microns, and those of the DC_3 pair by 63 ± 4 microns. DC_2 lies slightly laterad of an imaginary line joining DC_1 and DC_3. The DC_2 pair are 125 ± 6 microns posterad of the DC_1 pair and the DC_2 pair are only 85 ± 5 microns behind the DC_2 pair. The ratio of these two distances, 1:1.47, is much smaller than that of many other *Bryobia* species, especially of the *praetiosa* complex in which the ratio varies from 1:1.11 to 1:1.28.

Acknowledgments

I wish to thank Dr. A. E. Pritchard, University of California, Berkeley, Calif., for the loan of several Russian papers.

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Principles and Methods of Zoogeography: The Field Approach

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Zoogeographic studies can be pursued in the laboratory or library, but far preferably should be largely based on careful, first-hand field work. A familiarity with species in the field is a prerequisite to a thorough understanding of both their zoogeography and their systematics. Naturally, knowledge of the actual relationships of the species, and of the geology and geographical history of the areas involved, are also prerequisites to a complete understanding of the zoogeography of a group of insects.

In field work, the ecological approach is of the greatest relevance. Specimens which are ecologically documented are much more valuable than ordinary museum specimens with only general locality, date and collector. Additional information, such as precise altitude, niche, host plant or host animal, feeding habits, immature stages, natural enemies, abundance — all may be extremely helpful in zoogeographic correlation. Apparent morphological similarities of geographically widely separated forms can well be balanced and checked by comparing these other criteria.

One of the primary essentials to solving zoogeographic problems is the assembling of adequate material. Too much taxonomic work of the past has been based on fragmentary collections, and many conclusions set forth have been somewhat ill-advised. Various cases of "discontinuous distribution" have proved to be more continuous than supposed, as intermediate links have been uncovered, or proven to be based on misinterpretation of apparent relationships.

One of the best methods of gathering adequate material is for a specialist to thoroughly understand the ecology of his group from a broad geographical viewpoint, and to spend long periods of time in the field. This should involve examining all appropriate niches over very wide areas. However, this would involve a great deal of time and expense, and few research workers can afford this. Another approach, which is fairly common, is to borrow all material available, from many museums, of the group concerned. This plan assumes that reasonable or equivalent field work has been done over major portions of the earth. This, of course, is not true, particularly in smaller and less attractive types of insects, which are generally overlooked by the general collector or amateur.

One plan to circumvent these short-comings (from the zoogeographical standpoint) of available museum collections is to organize a broad-scale survey for an appropriate zoogeographical area. This can be done by having experienced field workers cover the area in stages, doing systematic general collecting in different localities, and attempting to sample all niches by various collecting methods. The field men should have wide experience, and broad general knowledge of various insect groups and their habits. First of all they should appreciate the importance of stressing small and minute species, and hidden niches, and of ecological documentation. It is primarily the larger and more ubiquitous forms that have already been taken by the early collectors, who have generally left the minute forms untouched unless their special interests happen to include small forms. Also, specialized methods of collecting, such as the use of Berlese funnels of different types; sifting; dredging; flotation; bagging or caging of various types of debris, nests, hosts, moss, wood, etc.; Malaise traps; large nylon nets suspended to rotate facing the wind; bait traps involving sweets, fermentation, carrion, excrement or other materials; bright light traps, including mercury vapor lamps; or other devices and methods, should be used.

Of course the simplest way to do general collecting is to do miscellaneous searching, or general sweeping, but with the addition of the preceding methods, the catch will be much richer and more varied, and more ecologically documented material can be assembled. To operate in rough country with varied equipment is not simple, and requires fairly long stays in each area picked, with short side-trips to work at different altitudes and to sample varied niches. There is of course advantage in operating with a team of two or three entomologists. Then there are the advantages of operating with a botanist or a vertebrate zoologist, for aid in identification, or collection, of hosts. In general, however, the large expedition is not necessarily favorable to operation in desirable areas, because of the difficulties of transport and supply in rough, wild country. It may prove much more appropriate for a single field man to camp at or near a patrol post or mission station for a considerable period, using local assistance, and for the program to maintain several field men separately. For entomological field work in many distant, tropical places, the cost of transportation to the area from home may prove to be a large part of the total expense. Thus the shorter the time-period of the trip, or the more people participating, the greater is the relative cost. It has proved appropriate in many areas for one worker to go for a considerable period, and to train local assistants, if trained ones cannot be engaged.

After a considerable period of this general type of coverage, using varied means of collecting, specialists should themselves sample selected environments to test the effectiveness of the general program, and to fill remaining gaps in the picture. The sampling by systematists themselves can of course be started without waiting for completion of the general collecting program. It is of course

very desirable to have general collecting done by systematic specialists, who appreciate the problems of zoogeographic study. Likewise, it is desirable for each systematist to do some of his own field work.

When operating on a general survey there is always the problem of dividing one's time between emphasis on general harvesting of the greatest number of specimens and species possible, and that of collecting as high a percentage as possible with accurate niche and host data. However, an effective compromise is possible by satisfactory training of local assistants and operation of mechanical devices or routine techniques, both for mass-collecting, such as light-trapping, Malaise trapping, mixed Berleseing, and general continuous sweeping (as opposed to netting, bottling and labelling separately from each plant or other niche), and on the other hand for separate rearing, baiting, sifting, searching, etc., of specific niches, which should be largely done by the trained entomologist. Obviously, this must be planned in terms of sufficient time in one locality, from the standpoint of the cost of transport of varied equipment, time lost in packing, moving and resetting of traps and other devices, and the training of local help. Obviously, the specialist collecting only his own group of interest, or only the insects that occur in the niches occupied by that group, or those to be collected by the same means, will get more species in such groups, and with a much higher percentage of ecological documentation. However, to get the same coverage for a broad geographical area, he would have to do a great deal of travelling and visit many places. This would probably prove more expensive and more time-consuming than filling gaps in a long-range intensive program.

In doing field work one should try to assess the role of each species in the particular niche. For instance, some species may be dominant, and others very restricted in range. Or one may replace another in more and more areas, and carry the latter to extinction, or allow it to survive only in areas unfavorable to itself. Thus two species of the same niche may seem to occur irregularly, but may actually be replacing each other, competing for the niche, or may be in the process of establishment in places where the niche has been unoccupied. This may consist of "island- or mountain-hopping", for instance, with different related species reaching the same niche on different isolated localities at different times.

Another problem is zoogeography is to learn why certain niches appear to remain unoccupied, even though they appear equivalent to similar, occupied niches, in the same general region. Here, again, experience and knowledge of ecology are important to the zoogeographer. The importance and effectiveness of natural enemies, as well as competitors, should not be underestimated. Also the question of population levels necessary for survival in an area are too little understood.

One very important question relevant to distribution is the vagility (potential for dispersal) of the members of a group, and the methods of dispersal. This is particularly pertinent in considering faunal relations of separate continents, islands and mountain ranges, or areas of similar rainfall, humidity or temperature separated by areas of contrasting climate and vegetation. For some groups of insects, this may be as important, or more important, than past geographical connections, and of course it must be related to climatic evolution. For oceanic islands, vagility and means of dispersal are of the greatest significance in analyzing insular fauna and in attempting to define relationships and origins.

Since most insects on the isolated oceanic islands are small and of relatively low specific gravity, and since they (or their winged relatives) are not strong fliers as a rule, it is assumed that most dispersal to such islands has been by air currents. For the greatly isolated islands, the frequent success of raft dispersal

seems unlikely, and the nature of the fauna of such islands seems to corroborate this.

In attempting to prove the thesis that most natural populating of isolated oceanic islands has been by passive dispersal through air currents, of insects prone to becoming air-borne, various experiments, as well as provisional faunal analyses, seem to give credence to the idea. Insects trapped in nets mounted on ships or airplanes prove to be largely small types, in general of the same groups represented in isolated environments. Some of these groups are wingless as adults. Also, it has been noted for the oceanic Pacific islands in general that in some groups the representatives established are primarily those which are nocturnal in flying habits, and thus more likely to become airborne during storms than those diurnal flying forms which hide when the sun is not out. Further that groups living in dead twigs, those mining in leaves, or living in other light parts of plants, or decaying debris, are more likely to be represented than those requiring growing plant tissue or sapwood, or those feeding unprotected on plant surfaces, boring in living plants, feeding in roots, or living in soil. For, as is obvious, those in the latter categories would be less likely to become airborne or to survive long raft travel and exposure to salt water. Most of the large, heavy-bodied native insects found on isolated islands may have originated from importations in pupal cells in elevated branches of large floating trees, or were carried by winds in sections of dry bamboo, or hollow pieces of palm-frond, or tree-fern leaf, mid-ribs. It is noticeable that such large species are few in species on distant islands.

In testing these theories, best success has been achieved by mounting large nets on ships crossing the ocean. These nets are of nylon organdie and are attached to large iron rings with small rings for attachment welded on two opposite sides. These nets can then be run up on flag-lines or suspended by ropes from other structures, singly or in series, and examined at intervals. The development of this method followed on experiments with frames bearing screens painted with adhesive mixtures, and with various metal and screen cylinders and funnels ending in screens, jars or bags, and with wind-sock bags rotating on vertical, solid axes. The advantage of the light nets on rings suspended by ropes is that they face the wind at all times and are easier to operate, more economical, cleaner, require less deck-space, and catch fewer contaminants from the ship itself. This type of trap is now being used on trans-Pacific ships, and in Antarctica, although to date nothing has been caught on the Antarctic continent. On the mid-Pacific, catches have been made far distant from land. Trapping from airplanes and helicopters has also been undertaken, with successful catches over land. Likewise, trapping has been done on atolls, but the catches cannot be interpreted until at least the local fauna is thoroughly known, and this may vary from time to time on atolls subjected to much outside communication.

The testing of these large nylon nets on land has shown that many small insects are blown, or fly, into the nets in good weather with moderate breezes. This suggests their possible use in general collecting, at strategic spots, as with a Malaise trap. In New Guinea considerable success resulted from stretching a Malaise trap across a small stream, which was used as a thoroughfare by many insects, not merely those associated with the water.

In summarizing, the importance of correct and complete field data, and exhaustive collecting, cannot be minimized in facing the problems of the insect zoogeographer.

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A Plastic Leaf-Cage for Rearing Insects on Whole Attached Leaves[1]

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At the Victoria laboratory a simple plastic cage was devised for rearing root weevil adults on whole attached strawberry leaflets. The cage (Fig. 1) was constructed from 10-dram plastic pill vials (Cunningham, Drug Stores Ltd., 1300 Douglas Street, Victoria, B.C.) having an inside diameter of one inch and length of three inches.

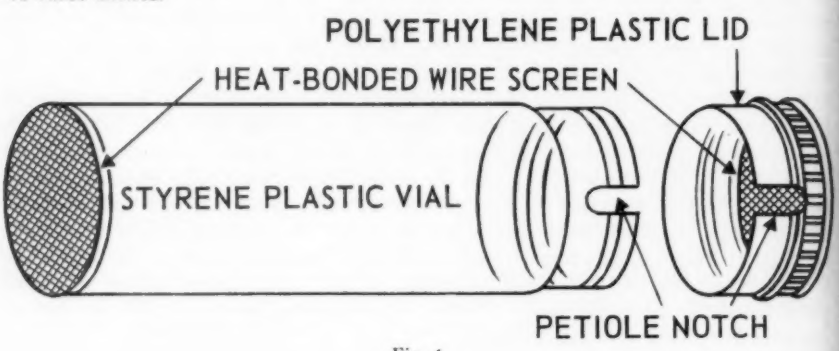

Fig. 1

The bottom of the hard styrene plastic vial was cut off with a band saw and the top of the soft polyethylene plastic lid was cut out with a sharp knife. Bronze screening of 44 mesh (number 60, strainer cloth supplied by Hickman Tye Hardware Co., Ltd., 910 View Street, Victoria, B.C.) was fastened to the bottom of the vial and to the top of the lid by placing 1⅛-inch squares of the screen on an electric hot plate and pressing the plastic parts onto the wire. The hot wire melted the plastic and became imbedded in it, forming a strong bond. The screen was trimmed with small tin snips and ground smooth on a grindstone. To facilitate attachment to growing leaves, a hot glass rod was used to melt a notch in the rim of the vial opening and lid large enough to accommodate the leaf petiole. An insect-tight seal was formed around the petiole in the notch when the lid was turned slightly.

The cages were supported by a 12-gauge galvanized wire stand made by turning one end of a 10-inch length around the vial and forcing the other end into the soil.

In the insectary the cages were easily examined for weevil eggs and rapidly changed to new leaves. The cage is not recommended for field use as condensation occurs on the inside walls. Other uses for the cage include collecting live insects and rearing insects on excised foliage in a chamber.

The cost of materials was about nine cents per cage.

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